

Boundary effects on the vertical ranges of deep-sea benthic species

JESÚS PINEDA*†

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Abstract—Since environmental gradients are more pronounced on the continental shelf and continental slope than in deeper waters, benthic deep-sea species occurring in shelf and slope regions should have smaller vertical (bathymetric) distributional ranges than species occurring in continental rise and abyssal regions. This paper explains a species' vertical range with a model that considers the existence of boundaries to species' vertical distribution (the deepest sea floor and the sea surface). The model assumes that a species' center of distribution corresponds to its mean depth of occurrence [(minimum depth of occurrence + maximum depth of occurrence)/2]. The model shows that the maximum vertical range must be dependent on the mean depth of occurrence. This value peaks at intermediate depths and decreases as one approaches either shallow or abyssal depths; the interaction of the shallow and abyssal boundaries with the endpoints of species' range produces a constraint envelope that precludes large ranges for species close to the boundaries. Data from different taxa show a relationship between mean depth of occurrence and vertical range for several taxa. Vertical range is small at continental slope (200–1500 m) and upper slope depths, increases with depth to a maximum at upper continental rise depths (1500–3500 m), and then contracts at lower continental rise (3500–4500 m) and abyssal plain (4500–6000 m) depths. Results suggest that boundaries to distributions can have an important effect on the bathymetric gradient of species vertical distributions.

INTRODUCTION

THE vertical gradients in physical, chemical and biological parameters from shallow to abyssal water depths (see SVERDRUP *et al.*, 1942, for examples) create a depth-dependent environment from the shallow continental shelf to the deep abyssal plain. This depth-related change in environment exerts a wide range of influences on the organisms (GAGE and TYLER, 1991, for a review), from the molecular to the ecological level. One might expect that this environmental gradient would affect the vertical distributional range.

The vertical distributional range of an aquatic species can be influenced by many biological and physical phenomena, operating on contemporary to evolutionary time scales. While the vertical range of benthic deep-sea species is frequently reported in the literature, it has received little attention as a phenomenon in its own right. VINOGRADOVA (1959) found that cosmopolitan benthic deep-water species are mostly eurybathic, while stenobathic species are confined to small depth ranges and restricted geographical distribution. VINOGRADOVA (1969) also proposed that species living deeper than 2000 m

*Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093-0208, U.S.A.

†Present address: Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A.

could be classified as stenobathic or eurybathic: species that occurred deeper than 2500–3000 m (“true abyssal species”) had small vertical ranges, species at less than 2500–3000 m (“bathyal species”) generally had large vertical ranges. SANDERS (1977) proposed a relationship between vertical range, zoogeographical range, physiological tolerance, tendency to speciate and other attributes for deep-sea ophiuroids, bivalves and crustaceans. Taxa with the largest vertical range have the broadest zoogeographical range, the greatest physiological tolerance and the least tendency to speciate, while taxa with the smallest vertical range have restricted zoogeographical range, least physiological tolerance and the greatest tendency to speciate. REX (1977) proposed that differences in vertical ranges among groups could be determined partly by biological interactions: populations at higher trophic levels have compressed vertical ranges because of interspecific competition, while those at lower trophic levels, which are controlled by predation, might have larger vertical ranges. Another approach (SIEBENALLER and SOMERO, 1989, for a review) asserts that protein pressure adaptations have a major role in influencing the vertical range and suggests that: “Although a variety of ecological and physical factors underlie the vertical zonation of species, hydrostatic pressure *per se* appears to play an important role in determining these patterns.” (SIEBENALLER and SOMERO, 1989, p. 1). The vertical range has most often been used in association with vertical zonation to corroborate or refute the hypothesis of discrete vertical zones of fauna (CARNEY *et al.*, 1983; HAEDRICH and MERRETT, 1990; GAGE and TYLER, 1991, for reviews).

The influence of depth-related gradients on the vertical range is illustrated by the equatorial submergence phenomenon (HAECKER, 1904, cited in EKMAN, 1953): the range of some deep-occurring species contracts in warm, low-latitude waters. As EKMAN (1953, p. 249) put it: “Submergence is simply a consequence of the animal’s reaction to temperature. Cold-water animals must seek colder, deeper water layers in regions with warm surface water if they are to inhabit such region at all”. Although it is generally believed that the vertical range is related to a vertical environment gradient (EKMAN, 1953; VINOGRADOVA, 1969; HESSLER, 1970; MENZIES *et al.*, 1973; SANDERS, 1979; HESSLER and WILSON, 1983; WILSON and HESSLER, 1987; HECKER, 1990; ETTER and REX, 1990, for examples), the idea has not been explored systematically.

The vertical range of a species (*VR*) is usually reported as the maximum depth of occurrence (*mx*) and the minimum depth of occurrence (*mn*)

$$VR = mx - mn.$$

It is assumed that species within this range will have a vertical center of distribution. That depth, however, is seldom known, and here will be estimated as mean depth of occurrence (*Md*), defined as

$$Md = \frac{1}{2} (mx + mn).$$

Md might be related to an “optimal depth”, with peak abundance; a more thorough consideration of *Md* is presented in the discussion. This paper considers then relationship between mean depth of occurrence (*Md*) and vertical range (*VR*) for benthic deep-sea taxa (taxa having their center of distribution deeper than 200 m). Patterns in the distribution of *VR* with depth were tested for consistency and general significance. A model is proposed to explain the relationship between *Md* and *VR*, and some ecological implications are discussed.

METHODS

VR and *Md* of species from several deep-sea taxa were plotted from vertical ranges taken from the literature. Species represented by five or fewer individuals and/or sampled two or less times were omitted from the analyses except for data from PEARCY *et al.* (1982), where due to the lack of appropriate information all species sampled more than twice were included. Frequency of *Mds* per depth interval of species included and omitted from the analyses were also plotted. In total, 42.3% of the species were omitted (see the legend of Fig. 7 for details). Only data sets including samples from abyssal depths were analysed. Two types of data sets were analysed: those representing an intensive study in a restricted area, and those accounting for the depth distribution of taxa throughout their range in a more general region (systematic surveys).

RESULTS AND DISCUSSION

In the following text, a model describing the relationship between *Md* and *VR* is presented. I then describe the patterns emerging from plotting *VR* vs *Md* for several deep-sea taxa, and substantiate that *Md* is a good estimator of the depth of maximum abundance. I later explore the implications of relaxing some model assumptions and finish by discussing the influence of other factors on *VR* and some implications of the results presented here.

The model: a geometric constraint

Consider the upper and lower portions of a bathymetric range that is symmetrical with respect to the mean depth of occurrence. This condition will be relaxed later. Consider also a set of species confined between two boundaries such as the sea surface and the deepest sea floor. It follows that species with a mean depth of occurrence closer to one of the boundaries will be constrained to having smaller vertical ranges than species equidistant from the boundaries. If the distance from the boundary to *Md* is small, the opposite symmetric range is correspondingly small (Fig. 1A). An important consequence is that while taxa with small *VR* can occur at any depth, species with large *VR* are constrained to having *Mds* at intermediate depths (Fig. 1); the interaction of the boundaries and the range endpoints of species produces a constraint envelope that precludes species close to the boundaries from having large ranges (Fig. 1B). Although the model is described for deep-sea basins, I suggest that it also could be applied in shallow basins or analogous terrestrial situations. For example, the upper and lower portions of the bathymetric ranges can be equated to species' range endpoints, *Md* can be replaced by the center of distribution of a species through an environmental gradient, and boundaries could include, for example, the top of a mountain and the seashore. PIELOU (1977) plotted geographic range span vs latitude of mid-point and presented a similar triangular constraint envelope; she offered, however, no further discussion regarding the implications of this triangular space.

The vertical range for each species $VR = mx - mn$ and the mean depth of occurrence $Md = \frac{1}{2}(mx + mn)$ are both defined by the same terms. A prominent characteristic of the model is that it is the *maximum* value of *VR* that can be determined either by the deepest or the shallowest boundary: assume that these boundaries have depths *MX* and *MN* (Fig. 1A). If *VR* is determined by the shallowest boundary, then the minimum depth of

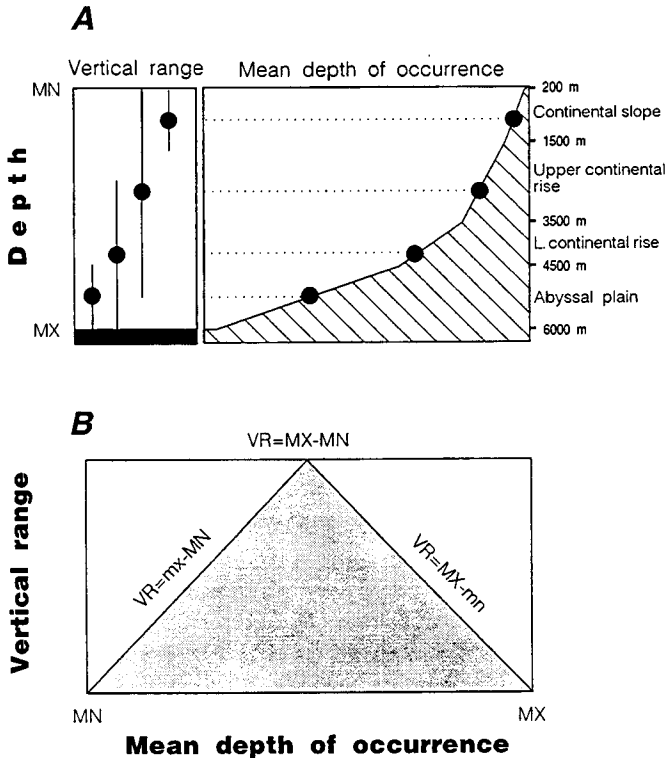


Fig. 1. Schematic representation of the geometric constraint model. Boundaries are denoted as MN (sea surface) and MX (deepest region) while mn and mx represent the minimum and maximum depth of occurrence of a species. Black circles represent species' mean depth of occurrence. The upper panel (A) shows species mean depth of occurrence and their vertical range. It is shown how the vertical range is determined by the proximity of a boundary. The vertical range is equal to two times the distance of the species Md to the closest boundary. The lower panel (B) is a schematic representation of the relationship between VR and Md . The triangular shaded area represents the constraint envelope for $VR - Md$ values. According to the model, VR values outside the triangle are impossible. Equations provide VR when the range is restricted by a boundary. The left side of the panel shows the case where the minimum depth of occurrence is equal to the shallow boundary, $mn = MN$, while the right side of the panel describes the case where $mx = MX$. Thus, a species with Md close to MX has a vertical range $VR = MX - mn$.

occurrence of a species, mn , equals the depth of the shallowest boundary MN . Thus, for $mn = MN$ it follows that $Vr = mx - MN = 2(Md - MN)$ and $Md = \frac{1}{2}(mx + MN)$. If VR is determined by the deepest boundary, then $mx = MX$, $VR = MX - mn = 2(MX - Md)$ and $Md = \frac{1}{2}(mn + MX)$ (see Fig. 1B). The maximum range is set by the presence of two features: (a) MN , the sea surface (and the directly adjacent rapid environmental change with depth); and (b) MX , the abyssal sea floor (sea floor area diminished exponentially beyond this region; see the legend of Fig. 8 for sea floor proportions). Although large VR s extending into hadal (>6000 m) depths are possible, they might be inconsequential because of the rarity of such zones.

If this model is to be useful for understanding the vertical ranges of benthic deep-sea organisms, one should examine if large VR s at intermediate depths are realized; the issue

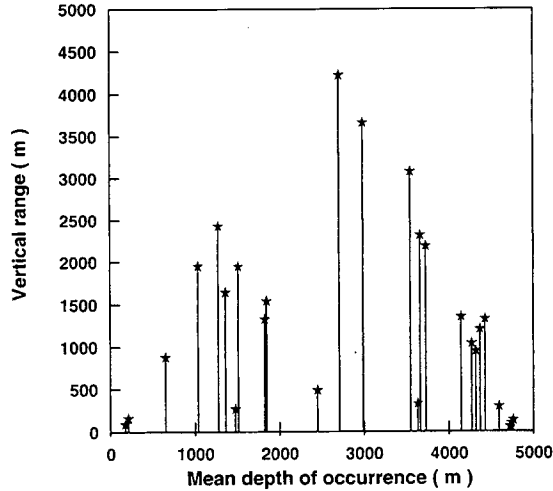


Fig. 2. Mean depth of occurrence – vertical range relationships for desmosomatid isopods from their known world distribution. Each symbol represents one species. m = meters. VR and Md were calculated from data in HESSLER (1970).

of symmetry of the upper and lower portion of the range with respect to Md also should be thoroughly examined.

Empirical relationships between mean depth of occurrence and vertical range

Figures 2 to 6 show the relationship between mean depth of occurrence and vertical range for several taxa. Large vertical ranges predominate at intermediate depths. Small vertical ranges occur at all depths, but they seem to occur more frequently at shallow or

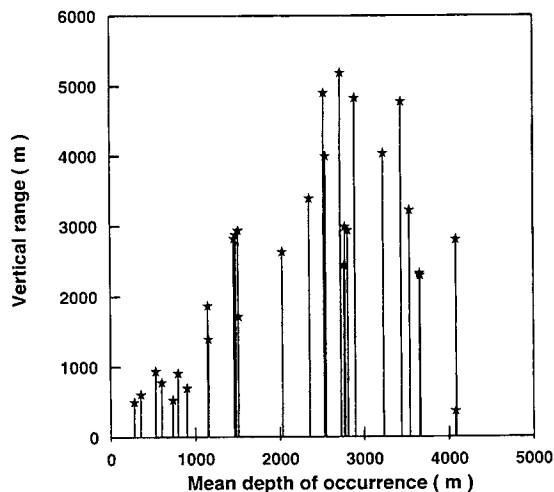


Fig. 3. Mean depth of occurrence – vertical range relationships for Sipuncula from the eastern Atlantic ocean. Symbols as in Fig. 2. Data from CUTLER and CUTLER (1987).

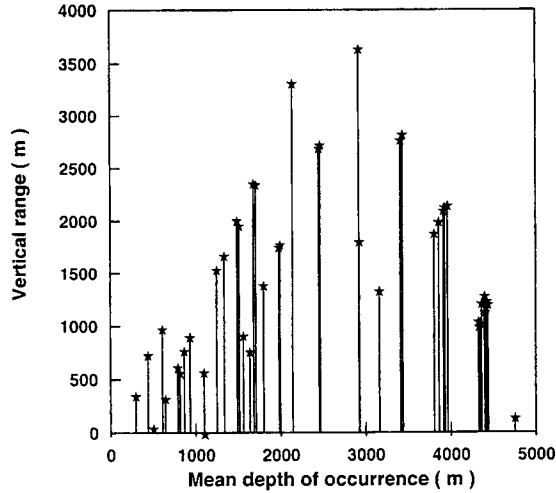


Fig. 4. Mean depth of occurrence – vertical range relationships for gastropods from the Gay-Head Bermuda transect. Symbols as in Fig. 2. Data from REX (1972) and M. REX (personal communication).

abyssal depths. A potential problem in omitting some taxa from the analyses is that larger VR at intermediate depths could result from having omitted a disproportionate large number of small-range species at upper continental rise depths. Also, because abyssal species are harder to sample, restricted ranges of abyssal species may be a sampling artifact. Figure 7 shows species included and omitted from each depth interval; in both cases, most species occur at shallow waters, with a relatively lower proportion omitted or

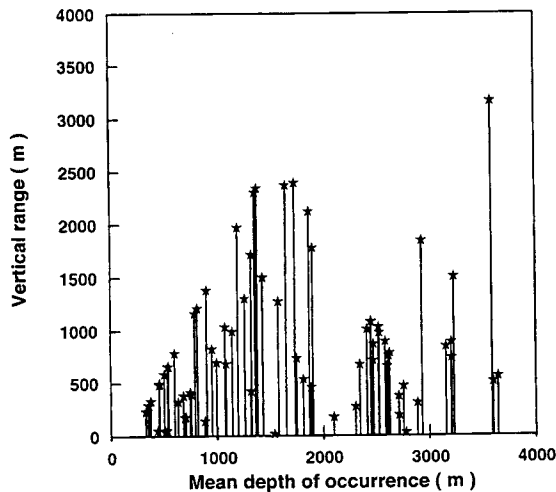


Fig. 5. Mean depth of occurrence – vertical range relationship for benthic fishes off Oregon. Symbols as in Fig. 2. Data from PEARCY *et al.* (1982); species whose *mn* was only identified as less than 400 m were assigned an *mn* = 200 m.

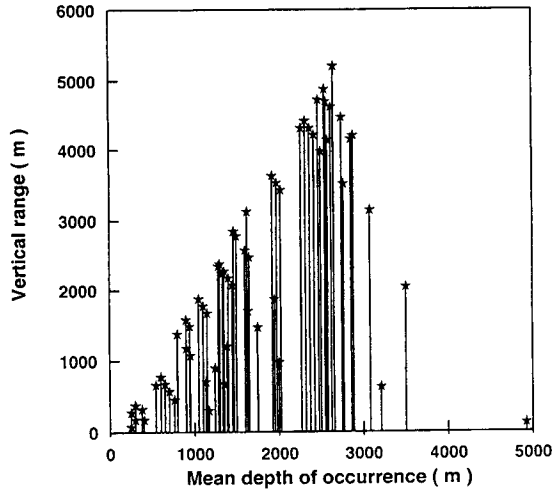


Fig. 6. Mean depth of occurrence – vertical range relationships for benthic polychaetes from the Gay-Head Bermuda transect and from off northeastern South America. Symbols as in Fig. 2. Data from HARTMAN (1965).

included from continental rise and abyssal depths. This suggests that the criteria for omitting species did not bias the analysis. The pattern in Figs 2–6 is substantial for sets of data involving intensive areal sampling and wide systematic surveys, but is more pronounced for some taxa than for others.

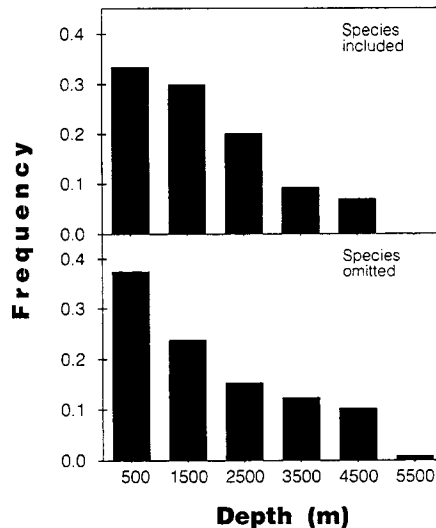


Fig. 7. Histograms of species number per depth interval for species included and omitted from the analysis. Species *Md* was used to assess species depth interval. Species omitted from the analysis ($N = 235$) were sampled in two or less stations and/or their total abundance was five or less individuals for desmosomatid isopods, gastropods, polychaetes and sipunculids, while fish taxa omitted were sampled in two or less stations. $N = 313$ for species included in the analysis. The proportion of species omitted are 12/38 for desmosomatid isopods, 92/152 for gastropods, 114/223 for polychaetes, 15/103 for fishes and 2/32 for Sipuncula.

The patterns in the plots could be taken as a mathematical artifact emerging from the forced relationship imposed between Md ($[mx + mn]/2$) and VR ($mx - mn$) because this produces a constraint envelope of possible values of Md for a given VR (as described by the model; see Fig. 1B). Consequently, any correlation or regression analysis between Md and VR , testing whether larger ranges predominate at intermediate depths, would be "spurious" because it would be based on combinations of the same parameters (KENNEY, 1982). If it is well supported, however, that mean depth of occurrence is a good estimator of the depth of maximum abundance, then this artifact would turn out to be a strong, limiting, ecological factor.

Center of abundance and distribution

Assuming that Md of populations correspond to their centers of distribution then populations with centers of distribution close to boundaries would be necessarily restricted to smaller ranges, relative to populations of intermediate depths, and the model would describe well the phenomenon in nature. The assumption implies symmetry of the ranges with respect to the center of distribution (this assumption will be relaxed below). To support the assumption, another hypothesis can be invoked: that the spatial center of abundance matches the center of distribution of species occurring on environmental gradients, and that densities decrease toward the edge of the ranges (HENGEVELD and HAECK, 1981, 1982) on a function resembling a Gaussian curve (WHITTAKER, 1967; BROWN, 1984; but see RAPOPORT 1982, for an alternative model); this model implies symmetric ranges and supports the assumption of the geometric constraint model, that species center of distribution can be estimated as Md . If populations have centers of distribution matching their centers of abundance, then ranges will be symmetric with respect to Md , and the effects of boundaries on range endpoints will determine VR .

The issue of the symmetry of the range with respect to the center of abundance has been documented for terrestrial taxa. WHITTAKER (1967), HENGEVELD and HAECK (1982), BROWN (1984), and SCHOENER (1987) concluded from empirical evidence that ranges of terrestrial taxa are generally symmetrical with respect to the center of abundance; HENGEVELD and HAECK (1981) proposed that two models could account for the pattern. The first model implies diffusion of vagile individuals from the center of distribution, while their preferred model proposes that the pattern reflects a "large-scale optimum response surface": higher densities occur at the environmentally determined optimum. BROWN (1984) proposed a similar hypothesis of a symmetrical range based on the following two premises: (a) the change of a population density over space reflects the change of the environmentally defined multidimensional niche; and (b), the environmental variables are auto-correlated, so that the probability of sites having similar environmental conditions is an inverse function of the separation among them. It then follows that species should have an optimum site. At increasing distance from this site, the particular combination of variables that define the niche will progressively change, and abundance will decline. BROWN (1984) also pointed out that the symmetry holds for spatial gradients with either low or high rates of environmental change, as the latitudinal geographic gradient or the intertidal height gradient.

It appears that benthic deep-sea taxa have depth distributions that are consistent with a model postulating the existence of a center of abundance (for examples see SULAK, 1982; THOMPSON *et al.*, 1987; HECKER, 1990). Nonetheless, exceptions might be expected (for

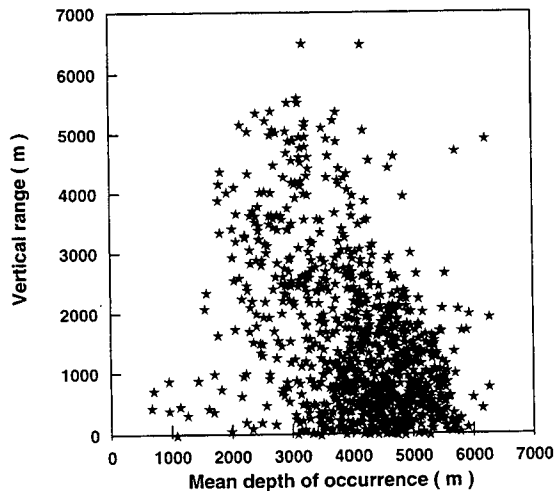


Fig. 8. Simulated mean depth of occurrence – vertical range relationships. mn and mx were obtained by simulating two sets of 980 depth points. For each pair of values the highest was equated to mx , the smallest to mn . Each mn or mx had a probability allotted proportionally to the hypsographic curve in intervals similar to those in SVERDRUP *et al.* (1942, Table 5), having removed depths less than 200 m. Within each depth interval, a uniform distribution was assumed. For depth intervals 200–999 m the probabilities equalled 0.047, for 1000–1999 m = 0.045, 2000–2999 m = 0.074, 3000–3999 m = 0.212, 4000–4999 m = 0.357, 5000–5999 m = 0.252, 6000–6999 m = 0.012 and ≥ 7000 m = 0.001. VR was calculated as $VR = mx - mn$, while Md was obtained from randomly sampling the interval $[(mn + \frac{1}{3}(mx - mn)), (mx - \frac{1}{3}(mx - mn))]$; a uniform discrete distribution was assumed.

example, BROWN, 1984). Sampling problems in the deep sea might preclude a rigorous test of this hypothesis.

Relaxation of the assumption

The assumption that the vertical range is symmetrical with respect to the center of distribution may appear extreme. Here, it is shown that for the geometric constraint to apply, VR need not be so restricted by symmetry. The geometrical constraint applies best when the center of distribution is well defined with respect to the range endpoints, even if it is not strictly symmetric. For example, if the center of distribution is defined as $Md = mn + \frac{1}{3}(mx - mn)$ or as $Md = mx - \frac{1}{3}(mx - mn)$ (Md close to the shallower or deeper extreme of the range), the curve will shift from symmetrical to asymmetrical left or right. The geometric model's consequence, that VR must be dependent of Md , would not apply if a center of distribution is lacking. In this case, the mathematical relationship between Md and VR would disappear. One example would be a species having similar densities across its range and then decaying abruptly.

For simplicity, the model assumes a single, fixed relationship for Md and VR . An important question, therefore, is whether similar results are obtained if variation among species in Md is allowed. This was tested by performing a simulation of relationships between VR and Md , introducing a random component for values of Md (see Fig. 8 for details). Figure 8 reveals that even with such random Mds , major aspects of the pattern

prevail: large vertical ranges are still confined to intermediate depths. Note, however, that in Figs 2–6 most species tend to track an upper limit or maximum possible value of their vertical range; according to the geometric model, those taxa have mn or mx close to one boundary. In Fig. 8 the simulated taxa do not track an upper limit; species whose mn or mx are not close to a boundary will be found below the upper value. This is the case here because the simulated mn and mx were randomly obtained, and the probability of mn or mx nearing MN or MX is small. This suggests that, broadly, mn or mx of real taxa are not randomly distributed but rather tend to be close to MN or MX .

The model is formulated for fixed values of MN or MX . It is clear, however, that the boundary that actually determines the upper range of deep-sea benthic species is not the sea surface with depth 0 m, but rather the rapid environmental change associated with shallow waters. The fact that MN is a diffuse rather than an unsurpassable boundary will result in species that do not perfectly track a maximum VR value in the relationships of VR to Md . Nonetheless, species could be clustered around this maximum value. In an analogous manner the deepest boundary is not a fixed depth nor is totally unsurpassable because there are always deeper areas available. However, the relative occurrence of the deepest areas is very small (Fig. 8). The large number of occurrences at 3000–6000 m depths reflects the large proportion of oceanic area.

Environmental gradients and the magnitude of the range

Several phenomena influence the vertical range other than the large-scale spatial geometric configuration of the ocean basins; the maximum value of VR , as described above, would only be attained if other factors do not restrict it. Examples abound where the vertical range of a species is correlated with geographic locality (for example see, EKMAN, 1953; HESSLER, 1970; HECKER, 1990). The best known explanation implies that VR is influenced by environmental depth gradients (for example see, EKMAN, 1953; VINOGRADOVA, 1969; HESSLER, 1970; MENZIES *et al.*, 1973; SANDERS, 1979; HESSLER and WILSON, 1983; WILSON and HESSLER, 1987; HECKER, 1990; ETER and REX, 1990). The general hypothesis could be phrased as follows: VR is proportional to the environmental rate of change. Species in shallow waters will experience a more rapid rate of change with depth in environmental properties than will those living at continental rise or abyssal plain depths, and therefore one can expect that VR will be constrained at continental shelf and upper slope depths. The environmental change at lower rise, abyssal plain and hadal depths should, in general, be smaller, and the corresponding VR should be large. Figures 2–6 show that, in effect, vertical ranges increase with increasing Md ; however, below intermediate depths, the range starts to decrease. The prediction that the ranges should increase inversely proportionally to the environmental rate of change cannot account for the decreased ranges at greater depths, but the result follows naturally from the geometric constraint; VR appears to be constrained by the abyssal boundary. Closer to the shallow water boundary it is difficult to assess any relative influence on the boundaries vs depth-gradient related effects because both models predict small VR s, but local (HECKER, 1990) as well as geographical (EKMAN, 1953; HESSLER, 1970) variations of VR imply that depth-gradient environmental factors are important. In summary, it seems that VR of species at continental shelf and upper slope depths might be influenced by both the environmental gradient and the shallow water boundary; at upper rise and abyssal depths, slow rates of environmental change let the constraints imposed by boundaries dominate.

Implications

This work partially corroborates VINOGRADOVA's (1969) assertion that deep-sea taxa could be classified into "stenobathic abyssal" or "eurybathic bathyal" species. However, another group should be added, those stenobathic species at continental shelf and continental slope depths. VINOGRADOVA (1969) did not specify the method used to classify species' depth zones. In this study, *Md* has been used to assess species position within the depth gradient. What other variables could be used to assess bathymetric species position? It is easy to demonstrate that using *mn* or *mx*, alone or combined, also would produce patterns in the vertical distribution of *VRs* (this results from *mn* and *mx* being non-independent with respect to *VR* and from assuming the existence of boundaries to species vertical distribution). An independent variable could be depth of peak abundance. Of course, if *VR* is related to depth of peak abundance (as has been argued above) then these two variables would become dependent; patterns in the bathymetric distribution of *VR* also could emerge. It is difficult to find a variable to assess bathymetric species position that does not involve *mn* or *mx*, the parameters used to estimate *VR*. In this paper, these pervasive relationships have been considered to argue that boundaries have a critical role in determining *VR*.

Some important implications emerge from the results presented here. The above discussion implies that the vertical center of distribution and the depth of peak abundance are important ecological variables of deep-sea benthic species. These are complexly determined variables influenced by several ecological and physiological variables that might interact further. The position of the centers of distribution and abundance are emergent species attributes that might elude simple reductionistic approaches; if these variables are determined by properties above the individual level, so is *VR* (see JABLONSKI *et al.*, 1985, for further discussion involving geographic ranges). That different taxa are arranged differently in Figs 2–6 implies important variation in ecological parameters among taxonomic categories. For one case, the proportion of stenobathic abyssal desmosomatids (Fig. 2) is relatively larger than the proportion of stenobathic abyssal polychaetes (Fig. 6). The relative dominance within a taxon of eurybathic or stenobathic species has been documented for several benthic deep-sea taxa (VINOGRADOVA, 1969, 1979; SANDERS, 1977; GRASSLE *et al.*, 1979), and while VINOGRADOVA (1969, 1979) suggested that this pattern reflects the antiquity of the fauna, SANDERS (1977) proposed a general life-history model. Trophic status also has been invoked to explain vertical range size difference between trophic categories (REX, 1977). The hypothesis, which could incorporate mobility and food selectivity (HAEDRICH *et al.*, 1980), proposes that predators could have small *VR* due to interspecific competition. Species at lower trophic levels, where interspecific competition could be relaxed by predation, might have larger vertical ranges.

It is interesting to evaluate recent hypotheses of latitudinal (STEVENS, 1989) and altitudinal (STEVENS, 1992) species diversity gradients in the light of the above discussion. In terrestrial environments, when latitudinal range is plotted as a function of the latitude where the organisms live, a simple positive relationship is found: tropical species have narrow geographical ranges while those living at high latitudes are less restricted (RAPOPORT, 1982). This is referred to as "Rapoport's rule" (STEVENS, 1989). For altitudinal comparisons (e.g. lowland vs mountaintop), the mean altitudinal range is positively correlated to elevation (STEVENS, 1992). These patterns run parallel with species' diversity

gradients in terrestrial environments: species richness is greater at both, lower latitudes and lowland areas. The hypotheses formulated by STEVENS (1989, 1992) to account for latitudinal and altitudinal diversity trends explain that species in the tropics and at the lowlands are adapted to narrow environmental conditions, making them more susceptible to microclimatic variations (turning the environment fine-grained) and therefore, more species can co-occur but have narrower latitudinal or altitudinal ranges. The work by REX (1981) supported former insights (VINOGRADOVA, 1962) and established the existence of a deep-sea diversity gradient correlated with depth. The pattern has been explained in different forms (see REX, 1981, for a discussion). Stevens' hypothesis associates environmentally determined geographic ranges and species diversity. The question, then, is whether Stevens' hypothesis helps to explain diversity peaks at intermediate continental rise depths. This hypothesis predicts that: (1) the environment with higher species diversity will contain those species with the smallest environmentally determined ranges; and that (2) without an environmental gradient, latitudinal species diversity gradients would not show up. In the deep sea, depths with the highest diversity contain species with largest VR, so the first prediction is refuted. The second prediction is tentatively refuted by the observation of HESSLER and WILSON (1983), that there is a latitudinal diversity gradient in the deep-sea isopods. (Results for other taxa may or may not substantiate this finding.) Therefore, Stevens' hypothesis, which might help explain latitudinal and altitudinal trends in species diversity in terrestrial environments, does not help to explain the deep-sea vertical diversity gradient.

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