Faunal changes with depth in the deep-sea benthos (9)

J. Frederick Grassle, Howard L. Sanders and Woolcott K. Smith

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 U.S.A.

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Abstract

A single method, the normalized expected species shared measure of similarity or NESS, is used to measure faunal change with depth for gastropods, cumaceans, polychaetes and ophiuroids. The standard errors of NESS estimates are calculated. Each group has a characteristic pattern of zonation on the Gay Head-Bermuda transect, with gastropods and cumaceans having much narrower depth distributions than either polychaetes or ophiuroids. In the polychaetes the higher similarity results from a small proportion of eurybathyal species. The greatest changes in faunal composition occur on the outer margins of the continental shelf at depths of 200 to 300 m and between upper slope and middle slope depths. These discontinuities coincide with the lower limit of the slope water at 200 to 300 m and the lower limits of temperature anomalies resulting from warm core Gulf Stream rings impinging on the bottom at slope depths. Cluster analysis methods tend to divide the samples into discrete groups or zones, even when the faunal similarity between stations appears to be a continuous function of depth. Changes in cumacean species with both depth and distance between ocean basins are compared for Eastern and Western basins of the North Atlantic.

Introduction

Species composition of deep-sea samples varies greatly with depth and relatively little with horizontal distance along depth contours (1). For this reason the description of depth zones has been a major focus of benthic investigations since the beginnings of deep-sea sampling (2). Zones have been described in a number of macrofaunal groups from the Gay Head-Bermuda transect across the North American Basin: polychaetes (3, 4, 1), protobranch bivalves (1), ophiuroids (5), desmometrid isopods (6), cumaceans (7), amphipods (8), and gastropods (9). The zonation of the epifauna large enough to be readily visible on the sediment surface (= mega fauna) has been described for the continental slope on the Gay Head-Bermuda transect (10, 11). George and Menzies (12) and Menzies, George and Rowe (13) have described isopod and megafaunal zonation from a Beaufort to Bermuda transect in the North American Basin.

Each of the cited works uses a different approach to the description of depth zones. The present study applies a single method to the classification of samples of cumaceans, gastropods, ophiuroids, and polychaetes from the Gay Head-Bermuda transect. This method uses clustering based on the normalized expected species shared method or NESS (14), which has been shown to be relatively unbiased and independent of sample size in comparison to other commonly used measures of similarity. By using a single method we will demonstrate the differences between taxa in depth zonation and the degree to which the fauna is distinctly zoned at various depths.

Methods

The similarity index, NESS, depends on taking random picks of a preset number of individuals from the original collection. The number of random picks is the sample size index or m (14). The expected number of species shared in random picks of size m is normalized by using the expected species shared in two random picks of m individuals within each collection. Since 2 m individuals are needed for calculation, m is normally approximately half the number of individuals in the smallest sample. A NESS similarity of one indicates a nearly identical proportion of species shared.

Since the similarity matrices are too cumbersome to present most of our results are given as cluster diagrams. The intensity of clustering depends on the combinatorial strategy adopted. Flexible sorting with the cluster intensity coefficient set at the commonly used value of -0.25 was employed (15, 16). Flexible sorting tends to produce distinct groups and underestimates the average similarity between large clusters. With the flexible group method, similarities between large clusters are near zero even when they share a number of species in common. Since rare species are an important consideration and the sensitivity of NESS to rare species depends on the value of m, we have used m = 50 in all but one of the results. This is as large a value of m as is practical without eliminating too many stations from the analysis. All of the samples consist of epibenthic sled hauls on transects in the North Atlantic (17, 18). Sieves with 0.42 mm mesh openings were used to process the samples.

Similarity estimates are based on a finite collection of individuals drawn from large unknown communities. In ecological and environmental studies, the evaluation of the sampling error for similarity estimates is an important and often overlooked problem. Unfortunately the few theoretical results available (19, 20) are not applicable to the NESS estimator. To estimate the sampling errors for NESS we have used an approximate method – the two sample jackknife (21). The method is straightforward but computationally complex. The basic procedure is to compute a set of NESS estimates by successively removing single individuals. The variability in these estimates can then be used to estimate the sampling variance (22).
Results

Figures 1–2 and 4–5 illustrate the NESS depth classification of each of the four taxonomic groups. The cumaceans and gastropods (Figures 1, 2 and 4) classify similarly except that there is a more distinct separation of the abyssal rise (2864–3834 m) from abyssal stations (>4000 m) in the gastropods. The fact that the additional stations included at m = 10 individuals (Figure 2) do not change the classification of gastropods indicates that gaps in sampling do not determine the groups in Figure 1. The cluster diagram for the cumaceans (Figure 4) includes samples taken in the Cape Verde, Brazil, and Canaries Basins, the Bay of Biscay (West European Basin) and the upper slope off Bermuda. All of the slope samples from basins other than the North American Basin (587 m–1896 m) and the single Bermuda slope sample (1153 m) classify separately from the Gay Head-Bermuda samples. The single deep sample from another ocean basin (3459 m in the Brazil Basin) clusters with the Gay Head-Bermuda transect samples of similar depths. The cumacean faunas of the slopes of ocean basins are more distinct zoogeographic entities than the ophiuroid or polychaete faunas (7). In both the gastropods and cumaceans the shelf (68 m–196 m) is sharply separated from the upper slope depths around 500 m. This is a region of rapid change of fauna with depth and the upper slope stations may be distinguished from the middle slope depths below 500 m in the gastropods and below 1000 m in the cumaceans.

The distinct zonation at depths shallower than 2500 m is shown in Figure 3. Similarity among each of three 500 m depth samples and similarity of each of three 4800 m
samples and every other sample are graphed in Figure 3. The points are connected for only one of the 500 m stations and one of the 4800 m stations. Stations immediately adjacent to any of the three 500 m samples show sharp reductions in similarity, whereas the 4800 m samples are quite similar to samples at approximately 3800 m despite depth differences of 1000 m.

Representative standard errors of the NESS estimates in Figure 3 are plotted for two of the stations. The error bars (22) indicate variation in similarity estimates resulting from drawing finite random samples from a homogenous population. In all of the deep station comparisons and most of the 500 m station comparisons the three samples fell within the 95% confidence limits or approximately twice the standard error illustrated. The cluster diagrams emphasize discontinuities in faunal composition with depth, however a plot of individual similarity indices as in Figure 3 emphasizes how continuously the fauna changes.

For the polychaetes and the ophiuroids separations with depth are less distinct (Figures 5, 6). The single polychaete shelf station classifies with the slope samples and the zonation within the slope region is less clearly defined than in the gastropods and cumaceans (Figure 5). Below 2500 m the zonation, although present, is not obvious. Four samples at approximately 4800 m station cluster together despite a wider spatial separation than the remaining samples at this depth. Individual species of polychaetes are characteristic of depth zones, however a cosmopolitan element of the fauna causes samples widely separated by depth to appear somewhat similar. Some of this similarity may result from lumping of species in the less well-studied families. Study of polychaetes from transects throughout the Atlantic is likely to result in major revisions of a number of groups.

The ophiuroid samples (Figure 6) separate into three groups: upper slope at approximately 500 m, middle and lower slope, and abyss at 2496 m and below. The broad depth distributions of most ophiuroid species are in sharp contrast to the cumaceans and gastropods and even the majority of polychaete species (18).

Differences between taxa in degree of similarity are best illustrated from similarities between pairs of stations (Table 1). The NESS similarities and approximate 95% confidence intervals are given for combinations of three samples where ophiuroids, bivalves, polychaetes, gastropods and cumaceans have all been analyzed.

Discussion

Each of the major taxa has a somewhat different pattern of zonation. These differences are likely to be the dispersal ability of species within each taxon (23, 18). On the basis of egg size ophiuroids are more likely to have planktonic dispersal than bivalves. The lowest rates of dispersal may be expected in the peracarid crustaceans which include the cumaceans since they brood their young. We still know little about dispersal in gastropods and polychaetes. However, rates of dispersal in some polychaete species appear high in recolonization experiments (24). While not rejecting the importance of life histories, Rex (9) has suggested that increased proportions of predators within a taxon may indicate increased interspecific competition and hence less overlap of species distributions with depth. Although cumaceans and other peracarids are not predators and have narrow depth distributions, the merit of this hypothesis cannot be adequately tested without more information on feeding behaviour of deep-sea animals.

The sharp change in faunal composition at the edge of the continental shelf at about 200–300 m has previously been noted for polychaetes, bivalves, gastropods and

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<th>Table 1. NESS similarities and approximate 95% confidence limits between samples: at 1102 m (Sta. C56 87), 1400 m (A12 73), and 3834 m (C56 85).</th>
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<td>3834 m vs.</td>
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<td>Ophiuroids</td>
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megalithal groups (1, 11, 9). This is near the lower depth limit of slope water in this region (25). The distinctness of the fauna in the region between 400 m and 1000 m has previously been noted by Haedrich et al. (11) and provides support for the concept of a transition zone on the upper slope (15). The sharp zonation of the fauna in this region may result from the effect of elevated temperatures in warm core rings impinging on the slope at depths in excess of 400 m (26). The boundaries between the remaining depth zones are not obvious and the issue of whether the fauna changes continuously or discontinuously (11) depends largely on the technique used in the analysis and presentation of results.

References
27. We thank George Hampson and numerous others for their dedicated efforts in processing samples. David Kravitz helped calculate the NESS error estimates.
28. Received October 31, 1977.