

A Numerical Model for the Formation of Fossil Assemblages: Estimating the Amount of Post-Mortem Transport Along Environmental Gradients

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In even the most sophisticated taphonomic studies, processes involved in the formation of fossil assemblages can rarely be directly observed, and are inferred from measurements and censuses of skeletal material. Here, we present a numerical model designed to permit direct evaluation, either alone or in combination, of various post-mortem effects on simulated fossil assemblages.

The primary objective of the basic model is to provide a realistic framework for species distributions, through several generations of accumulation, on the sea floor. The model establishes two "communities," each containing 25 species and 10,000 individuals per generation, along an "environmental" gradient. Species are assigned randomly to one of five ecologic tiers, and relative abundances are determined using MacArthur's random niche-boundary distribution. With respect to the gradient, geographic centers of abundance and ranges of distribution are also preassigned; they vary from species to species, within limits, to reflect the intergradational nature of the communities. Using these "guidelines," individuals belonging to each species are placed randomly or contagiously on a two-dimensional, 50 by 800 coordinate grid; the model is run through 50 generations to develop a time-averaged accumulation that can be sampled for numerical analyses.

The power of the basic model is that it can be manipulated to simulate a variety of taphonomic processes, and the results can be compared directly to patterns that would have resulted without the taphonomic overprints. In this initial use, we analyze the effects of limited amounts of post-mortem transport on faunal distributional patterns. Comparisons of transported and untransported accumulations permit the testing of a procedure for de-

tecting the amount of post-mortem skeletal transport along environmental gradients. To demonstrate its utility, this procedure is applied to a data set of subfossil molluscan remains from St. Croix, U.S. Virgin Islands.

INTRODUCTION

Renewed emphasis on research in taphonomy has markedly improved our ability to interpret the myriad processes potentially involved in the formation of fossil assemblages. Among the recent contributions are several comparative analyses of ancient deposits that have permitted rigorous assessments of spatial and temporal variations in taphonomic processes and effects (e.g., Kidwell and Aigner, 1985; Kidwell, 1986, 1988; Brett and Baird, 1986; Speyer and Brett, 1986, 1988; Norris, 1986; Parsons et al., 1988; Meyer et al., 1989). At the same time, a series of sophisticated actualistic investigations (e.g., Cummins et al., 1986, a, b; Allison, 1986, 1988; Fürsich and Flessa, 1987; Miller, 1988; Davies et al., 1989; Parsons, 1989) has helped to extract and quantify several important attributes of fossil preservation and accumulation.

Nevertheless, even with studies conducted on Recent assemblages and specimens, many taphonomic processes cannot feasibly be observed directly; their roles must be inferred from measurements on accumulated remains. The purpose of this paper is to present, and demonstrate the initial utilization of, a numerical model for the accumulation of benthic marine skeletal remains that permits direct measurement of particular taphonomic effects on spatial patterns in resulting fossil assemblages. The model also enables evaluation of a single taphonomic process in isolation from all others. In the real world, this is not easily accomplished because fossil assemblages often show the

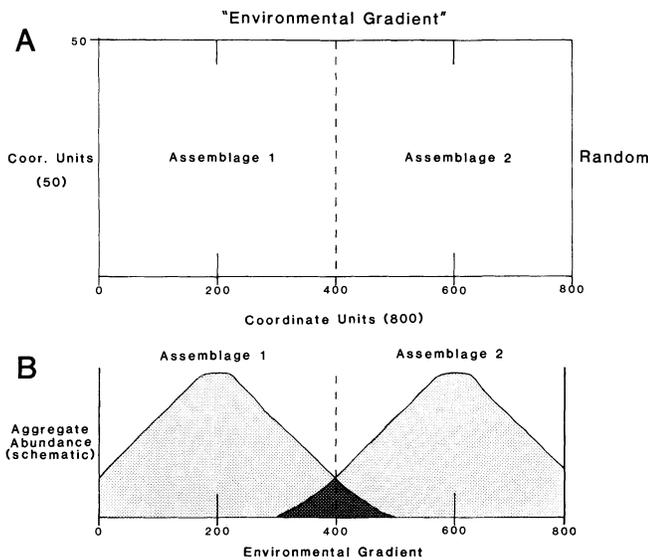


FIGURE 1—**A**) Map view of 50 by 800 model coordinate system, showing zones occupied by assemblages 1 and 2. The dashed line at coordinate unit 400 on the gradient axis symbolizes the species overlap at the interface between the assemblages. The vertical axis on the figure is termed a “random” axis because placement of individuals in this dimension is based solely on the generation of random numbers, without overprints of probability distributions (see text). **B**) Cross-sectional view of the modeled gradient, illustrating schematic, aggregate abundances of all species in assemblages 1 and 2; note the overlap near coordinate unit 400. Because of a built-in probability distribution, *centers of gradient distribution* for assemblage 1 tend to be most highly concentrated near coordinate unit 200, and those for assemblage 2 are most concentrated near unit 600.

overprints of several processes, the effects of which are difficult to unravel from one another. Moreover, the model allows direct comparison of an assemblage that has been subjected to modeled taphonomic process(es) to the assemblage that would have resulted had the process(es) not taken place; this is particularly useful for direct measurement of taphonomic effects.

This presentation is divided into two sections. First, we present the basic model, without the overprint of taphonomic effects, to fully explain its theoretical and numerical underpinning. In the second section, we utilize the model to help develop and test a methodology for determining, with some precision, the amount of post-mortem skeletal transport along environmental gradients.

BASIC MODEL

In constructing the basic model, the primary objective was to provide a realistic framework for species distributions, through several generations of accumulation, along an environmental gradient on the sea floor. This model could then serve as a “template” upon which various taphonomic processes might be applied and tested. Schematic representations of the model are presented in Figure

1A, B; individuals belonging to two intergrading faunal assemblages (“communities”) are placed in a 50 by 800 coordinate grid system (Fig. 1A; map view). Placements of individuals along the shorter axis are fixed randomly, but positions with respect to the longer axis are determined with the overprint of a modeled gradient. For each modeled species, the concentration of individuals is apt to be greatest near its *center of gradient distribution*. This center, in turn, is predetermined utilizing a probability distribution (see below) that, for assemblage 1, increases the likelihood of its location in the vicinity of coordinate unit 200, and, for assemblage 2, near coordinate unit 600. Thus, aggregate abundances for assemblages 1 and 2 will tend to be greatest near these points and decrease away from them, with spatial overlap near the center of the axis (coordinate unit 400; Fig. 1B). This intergradational aspect is reflective of the probable distributions of most soft-bottom marine assemblages along environmental gradients (see Whittaker, 1975; Cisne and Rabe, 1978; Springer and Bambach, 1985; Miller, 1988). Whereas the number of recognizable assemblages along any real environmental gradient might substantially exceed two, the use of just two assemblages is sufficient to investigate many taphonomic questions. Future versions of the model may incorporate an enlarged gradient dimension and a larger number of assemblages as warranted.

Much of the data presented in tables and figures below were generated as output during a single “run” of the model. The illustrated run serves to explain the development and calculation of model parameters, and also provides a baseline for comparison with results from the subsequent modeling and analysis of transport. This model does not generate a unique solution. Additional runs would likely produce outcomes that differ somewhat from the illustrated solution; the significance of this variability is considered later.

Model Parameters

Species Richness and Relative Abundances

For a single generation of the model, 10,000 individuals belonging to 25 species are assigned to each of the two assemblages. Although the selection of these values is somewhat arbitrary, the goal is to balance two concerns: 1) to generate spatial patterns that can be reliably analyzed statistically; and 2) to avoid “overcrowding” the simulation. For the purposes of both these objectives, the chosen species richness and relative abundance values have proven to be rather effective.

Relative abundances for individual species are determined utilizing MacArthur’s (1957, 1960) random-niche boundary (“broken-stick”) distribution, where the abundance of the r^{th} rarest species in an assemblage of m individuals containing n species is:

$$(m/n) \sum_{i=1}^r [1/(n-i+1)]. \quad (1)$$

TABLE 1—Attributes of species in modeled assemblage 1 for the illustrated run.

| Species | Abundance | Center of gradient distribution | Spreading coefficient | Maximum clump size | Tier |
|---------|-----------|---------------------------------|-----------------------|--------------------|------|
| A | 16 | 174 | 1.36 | 8 | 4 |
| B | 33 | 198 | 1.66 | 2 | 2 |
| C | 50 | 247 | 1.48 | 6 | 2 |
| D | 68 | 182 | 1.83 | 8 | 2 |
| E | 87 | 135 | 1.09 | 2 | 2 |
| F | 107 | 9 | 1.07 | 9 | 3 |
| G | 128 | 78 | 1.57 | 3 | 2 |
| H | 151 | 270 | 1.13 | 9 | 1 |
| I | 174 | 177 | 1.46 | 6 | 4 |
| J | 199 | 268 | 1.71 | 9 | 3 |
| K | 226 | 147 | 1.08 | 9 | 1 |
| L | 254 | 351 | 1.53 | 4 | 4 |
| M | 285 | 234 | 1.03 | 4 | 2 |
| N | 318 | 190 | 1.20 | 9 | 2 |
| O | 355 | 94 | 1.68 | 9 | 5 |
| P | 395 | 58 | 1.10 | 2 | 1 |
| Q | 439 | 344 | 1.14 | 5 | 4 |
| R | 489 | 136 | 1.48 | 4 | 4 |
| S | 546 | 283 | 1.22 | 9 | 2 |
| T | 613 | 266 | 1.41 | 7 | 2 |
| U | 693 | 209 | 1.04 | 1 | 4 |
| V | 793 | 263 | 1.15 | 9 | 4 |
| W | 926 | 193 | 1.80 | 6 | 5 |
| X | 1126 | 146 | 1.76 | 5 | 2 |
| Y | 1526 | 143 | 1.65 | 9 | 4 |

TABLE 2—Attributes of species in modeled assemblage 2 for the illustrated run.

| Species | Abundance | Center of gradient distribution | Spreading coefficient | Maximum clump size | Tier |
|---------|-----------|---------------------------------|-----------------------|--------------------|------|
| a | 16 | 641 | 1.05 | 7 | 1 |
| b | 33 | 688 | 1.64 | 3 | 2 |
| c | 50 | 500 | 1.31 | 7 | 5 |
| d | 68 | 442 | 1.12 | 5 | 2 |
| e | 87 | 665 | 1.88 | 5 | 5 |
| f | 107 | 644 | 1.73 | 1 | 2 |
| g | 128 | 535 | 1.70 | 5 | 3 |
| h | 151 | 490 | 1.94 | 6 | 1 |
| i | 174 | 654 | 1.54 | 2 | 5 |
| j | 199 | 463 | 1.10 | 9 | 5 |
| k | 226 | 654 | 1.12 | 5 | 3 |
| l | 254 | 599 | 1.22 | 5 | 4 |
| m | 285 | 637 | 1.23 | 2 | 4 |
| n | 318 | 635 | 1.15 | 5 | 1 |
| o | 355 | 690 | 1.43 | 1 | 1 |
| p | 395 | 517 | 1.64 | 4 | 5 |
| q | 439 | 700 | 1.59 | 3 | 4 |
| r | 489 | 688 | 1.68 | 2 | 2 |
| s | 546 | 650 | 1.09 | 3 | 2 |
| t | 613 | 515 | 1.62 | 6 | 4 |
| u | 693 | 585 | 1.95 | 1 | 5 |
| v | 793 | 594 | 1.69 | 7 | 3 |
| w | 926 | 640 | 1.83 | 7 | 3 |
| x | 1126 | 557 | 1.23 | 5 | 4 |
| y | 1526 | 539 | 1.52 | 6 | 1 |

Computed abundances for species in each assemblage are listed in Tables 1 and 2 (throughout this paper, species in assemblage 1 are designated by capital letters A through Y and those in assemblage 2 by the corresponding set of lowercase letters). Because these assemblages contain the same numbers of species and individuals, their relative abundance lists are identical.

Species relative abundances could have been generated using other well-known models such as Preston's (1948, 1962a, b) lognormal distribution. Analyses of fossil assemblages suggest, however, that no single model is consistently more appropriate than another (Schwartz and Sepkoski, 1977). In any case, utilization of the lognormal distribution would have little effect on the outcome or interpretation of the simulation.

Centers of Gradient Distribution

As noted earlier, species are individually assigned *centers of gradient distribution* (Tables 1 and 2); these remain in effect through the duration of a simulation and ultimately help govern the placement of individuals along the gradient (see below). Centers are determined by generat-

ing, for each species, a random number under the umbrella of a probability distribution produced by the equation:

$$s = 100 - 0.5d, \tag{2}$$

where *s* represents the relative probability that a point located *d* units from the predetermined geographic center of the entire assemblage (coordinate unit 200 for assemblage 1 and 600 for assemblage 2) will be selected as the center for the species. For example, in the case of assemblage 1, the calculated value of *s* for coordinate unit 200 equals 100, while that for coordinate unit 100 equals 50. Thus, coordinate unit 200 is twice as likely as 100 to be "randomly" chosen as the center for any species in assemblage 1. In this way, the process favors selection of centers near units 200 and 600, but by no means precludes centers far removed from these two points: for assemblage 1, the 25 selected centers for the illustrated run range from units 9 (species F) to 351 (species L).

Spreading Coefficients

Whatever their relative abundances, it is evident that, in nature, the spatial ranges of species vary substantially.

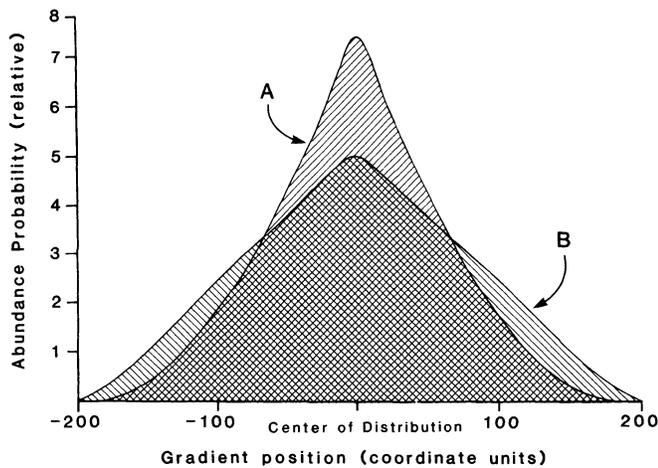


FIGURE 2—Two hypothetical species abundance-probability distributions, superimposed to illustrate the effect of the *spreading coefficient*; the value for the spreading coefficient is higher for distribution **A** than it is for **B** (see equation 3, in text). Individuals are more likely to be placed near the *center of gradient distribution* for **A** than would be the case for **B**.

Some are rather diffusely distributed, while others are more tightly confined, environmentally and spatially. To accommodate this variability, the model assigns randomly to each species a *spreading coefficient* that has a value between 1 and 2 (Tables 1 and 2). This coefficient affects the amount of “spread” in abundance around the species center of gradient distribution (Fig. 2). The larger the coefficient, the greater the likelihood that individuals of a particular species will be located near the species’ center (see description of placement of individuals, below).

Maximum Clump Size

Whittaker (1975) noted the tendency for individuals of a species to be distributed spatially in discrete clumps; this appears to be the case for most benthic marine organisms (Cummins et al., 1986a). This tendency is incorporated into the model by selecting a random integer value between 1 and 10 for each species as its *maximum clump size*. In nearly all cases, the average clump size for a species will be lower than the potential maximum; actual size is determined on a case-by-case basis as individuals are assigned to the coordinate grid (see below). Thus, there is likely to be variability in the sizes of clumps that comprise a single species, as well as differences among species in their average clump sizes.

Ecologic Tiers

All the parameters discussed thus far have been presented in the context of the 50 by 800, two-dimensional grid system. However, marine associations are obviously three-dimensional; various species are adapted for life above, at, or below the sediment-water interface. This three-

dimensional framework was most effectively formalized in a series of papers by Ausich and Bottjer (1982, 1985; Bottjer and Ausich, 1986), who recognized several epifaunal and infaunal *tiers* and provided a detailed history of changes in tier structure through the Phanerozoic. The existence of tiers is of relevance here for two primary reasons:

1) In the process of forming a fossil assemblage, either gradually or catastrophically, it is highly likely that individual tiers will collapse: soft-bottom fossil assemblages only rarely preserve the three-dimensional structure of the living associations from which they were derived. However, tiering in the living association permits species to spatially “overhang” or “underlie” one another, potentially increasing the species richness relative to that of a hypothetical association of comparable areal extent that has just a single tier. This may ultimately affect the species richness contained in a unit volume of accumulated fossil assemblage regardless of whether the tier structure is preserved.

2) Different tiers in a given association will not be subject to an identical suite of taphonomic processes upon death. For example, in some cases, epifaunal elements are more heavily subjected to biostratinomic processes than deep, infaunal elements because the infaunal elements are already buried (although they may be subject to exhumation during life or after death).

Thus, the model incorporates ecologic tiering as a third dimension; this is accomplished by randomly assigning each species to one of five “parallel,” 50 by 800 planes (Fig. 3) at the start of the simulation (Tables 1 and 2). In this basic version, no differential taphonomic attributes are assigned to any of the tiers; none are designated as “infaunal” or “epifaunal.” Future research into the taphonomic effects of tiering will certainly incorporate such attributes as well as explore the effects of simply varying the number of tiers. The inclusion of this third dimension provides the framework in the context of the model for ultimately carrying out these analyses.

Running the Model

Placement of Individuals During a Single Generation

The parameters illustrated in Tables 1 and 2 play integral roles in the placement of individuals within the three-dimensional model framework. Assignment of individuals is carried out, one species at a time, utilizing the following guidelines:

1) Based on the preselected value for the species, the proper tier level is located.

2) As a first step in placing an individual on the coordinate grid for the selected tier, a pair of random numbers is generated. The first determines where, along the 50 unit “random” axis, the individual will be placed. The second governs where the individual will be located along the “gradient” axis, under the auspices of a probability distribution generated with the equation:

$$U = (10 - 0.05f)^c, \quad (3)$$

where U represents the relative probability that the individual will be located f coordinate units from the *center of gradient distribution* for the species; C is the predetermined spreading coefficient. This distribution is highly comparable to that generated by equation (2), except for the incorporation of the spreading coefficient, which has the effect of narrowing or broadening the distribution as illustrated earlier (Fig. 2). The larger the value for the spreading coefficient, the greater the accentuation on placement of individuals near the center of the species' gradient distribution.

3) Once the initial individual is placed, the predetermined *maximum clump size* for the species is noted. If this value equals 1, then step (2) is simply repeated again and again until all the individuals belonging to the species have been placed on the coordinate grid. However, if the maximum clump size is greater than 1, then the model may place additional individuals in cells on the grid immediately adjacent to the first individual, up to the maximum clump size. This is accomplished by "fanning out" from the location of the first individual to some number of adjacent cells corresponding to the maximum clump size for the species. At each cell, a random number is generated to determine whether an individual of the species will be placed there; by design, the probability of placing an individual in the cell is equal to the probability that the cell will remain empty. Using this methodology, a clump of individuals may be generated, and it is possible for the clump to be any size up to the designated maximum clump size for the species. After the clump has been filled out, steps (2) and (3) are repeated until all the individuals belonging to the species have been assigned to the coordinate grid.

Using this sequence of steps, individuals belonging to each species are assigned to points on their respective tiers during a single generation of the model. It must also be noted that once an individual has been placed on the coordinate grid, it has "squatter's rights"; it may not be displaced from that point for the remainder of the generation. If, in the process of carrying out step (2), an occupied cell is encountered, then this step is repeated until an empty cell is located. On the other hand, if an occupied cell is encountered while filling out a clump [step (3)], then the cell is bypassed and the model simply continues evaluating any remaining cells that would potentially constitute the clump.

The incorporation of equation 3 promotes the generation of species distributions along the gradient that are approximately symmetric about the *center of gradient distribution*. This is in keeping with the observation that, in nature, species abundance curves along environmental gradients tend to be unimodal, approximating bell-shaped or Gaussian forms (see discussion in Gauch, 1982). Historically, simulations of species abundances along modeled gradients (coenoclines) have utilized formulae that generate Gaussian curves (e.g., Swan, 1970; Gauch and Whitaker, 1972). The design of the present model differs from that of earlier simulations in the utilization of random numbers in the placement of individuals. Gauch (1982)

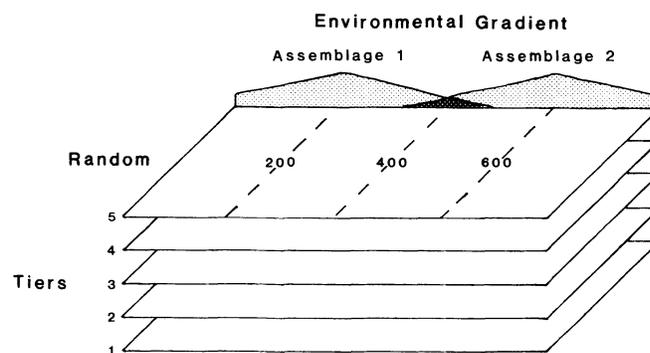


FIGURE 3—"Perspective" plot, illustrating the three-dimensional aspect of species placement by the model. Because of the provision for ecological tiering, there are five, parallel coordinate grids in a single generation of the model, and each species is randomly assigned to a single grid.

observed that field data tend to be noisy, and the use of random numbers is in keeping with the observation that the exact location of individuals is dependent not only on measurable physical and biological factors, but on chance as well.

To illustrate the placement of modeled species in the coordinate grid, a small portion of tier 4 for a single generation of the model is shown in Figure 4 (map view). Because this part of the grid is close to the geographic center of the environmental dimension (coordinate 400), it is within the zone of overlap for assemblages 1 and 2; individuals belonging to both assemblages (capital letters for assemblage 1, lowercase letters for assemblage 2) have been placed here. The most abundant species in this figure is Q , which, not coincidentally, has a *center of gradient distribution* near this part of the grid (344; Table 1). Note that species Q is distributed in clumps that range in size up to its *maximum clump size* (predetermined as 5; Table 1).

Accumulation Through 50 Generations

The model attributes and steps described above produce spatial distributions in two intergrading associations during a single generation. However, the primary goal of the model is to understand processes involved in the formation of fossil assemblages; clearly, an important attribute of such assemblages is that they are the time-averaged remains of not just one, but several generations on the sea floor (Walker and Bambach, 1971; Peterson, 1976, 1977; Warne et al., 1976; Staff et al., 1986). To incorporate time-averaging, the model accumulates individuals through 50 generations; graphically, the result can be depicted as a stack of 250 coordinate grids (5 tiers per generation through 50 generations; Fig. 5). No post-mortem transport or other taphonomic effects are included in this basic model, and the assumption is that, as they die, individuals will accumulate on the sea floor precisely, in map view, where they lived (incorporation of transport is discussed later).

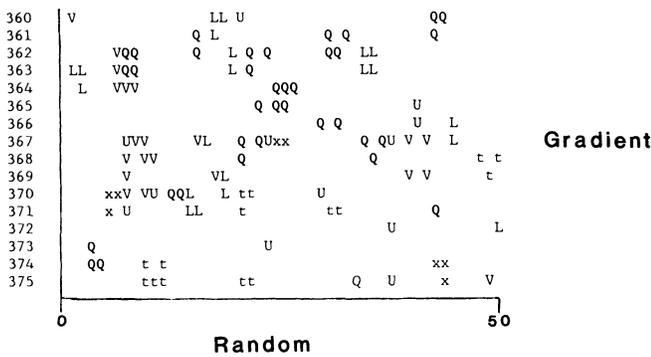


FIGURE 4—Map view of tier 4 (gradient coordinate units 360 through 375) for one generation of the illustrated run of the model. The most abundant species on this portion of the grid is species Q, which has a center of gradient distribution nearby, at coordinate unit 344. Note that individuals belonging to assemblages 1 and 2 are both present; the geographic center of the gradient axis is nearby, at coordinate unit 400.

Species attributes described above remain “in force” for all 50 generations. However, the exact placements of individuals within designated tiers can vary substantially from generation to generation because they are controlled not only by primary species attributes, but also by the production of random numbers that govern the exact locations of individuals or patches of individuals. In all, 1 million individuals belonging to 50 species are placed in the coordinate system during one 50-generation run of the model (20,000 individuals per generation).

Sampling and Evaluating the Outcome

Spatial Patterns

The results produced by the basic model can be sampled for numerical analyses using methodologies analogous to, and appropriate for, the sampling of subfossil accumulations on the sea floor; the exact spatial design of sampling depends ultimately upon the kinds of questions being asked. Because the primary concern in this instance was with the role of post-mortem transport along environmental gradients (see below), a sampling methodology comparable to that of Miller (1988) was utilized here. A transect that runs the length of the gradient dimension was established (Fig. 5), and it was sampled at 10-unit lateral increments. At the 80 sample stations, faunal composition was determined by “identifying” and tallying all the individuals present in the stacked, vertical column of 250 grid points produced by the model; in effect, each sample thus comprised a complete “core,” one grid point in diameter, through the model output.

Abundance curves for four selected species (including Q) along the transect are presented in Figure 6. Abundances of each species tend to be greatest near their respective centers of gradient distribution (see Tables 1 and 2). The curves are by no means smooth, which is reflective

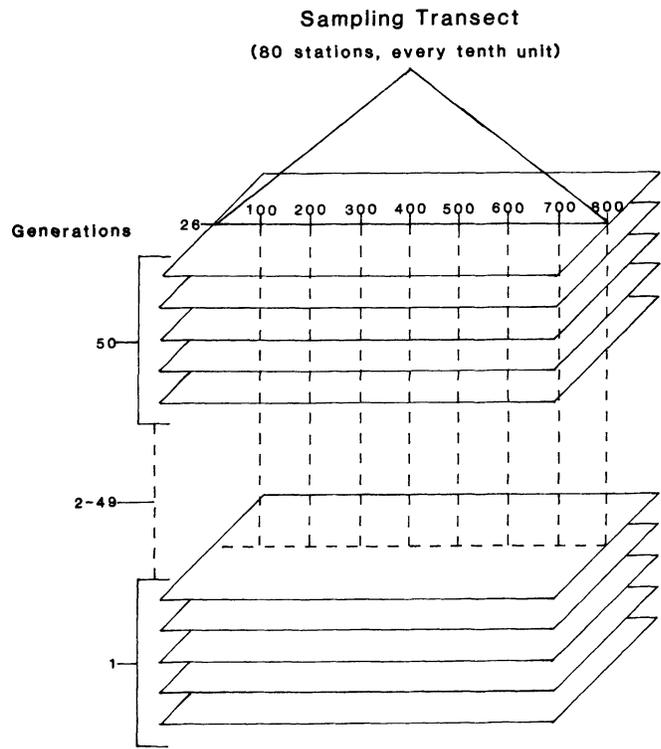


FIGURE 5—“Perspective” plot, illustrating the accumulation of individuals through 50 generations. For the purposes of sampling the outcome, a transect is established at the midway point on the “random” axis. It runs the length of the gradient axis and is sampled at ten-unit intervals. A sample comprises all individuals present in a one unit by one unit “core” through all 250 planes generated by the model.

of species abundance curves generated with actual field data (Gauch, 1982; Fig. 5 of Springer and Miller, 1990).

The 80 sample by 50 species data matrix developed with this sampling procedure can be analyzed numerically to evaluate compositional patterns and variability among the samples; a dendrogram from Q-mode cluster analysis of these data for the illustrated run is presented in Figure 7. With respect to sample variability, this dendrogram exhibits three notable attributes:

1) There is substantial “geographic” cohesiveness to the nine delineated clusters, although some samples, from a compositional standpoint, appear out of place. For example, based on compositional similarity, sample 250 is grouped with samples 140 through 220 in cluster 3, rather than with its nearest neighbors, which are contained in cluster 4. Nevertheless, individual clusters tend to be composed of samples that are in relative geographic proximity on the gradient.

2) The ordering of clusters on the dendrogram is geographically systematic with respect to the positions of samples along the gradient (see detrended correspondence analysis, below).

3) Within individual clusters, there is little systematic geographic ordering. For example, only 16 of the 80 sam-

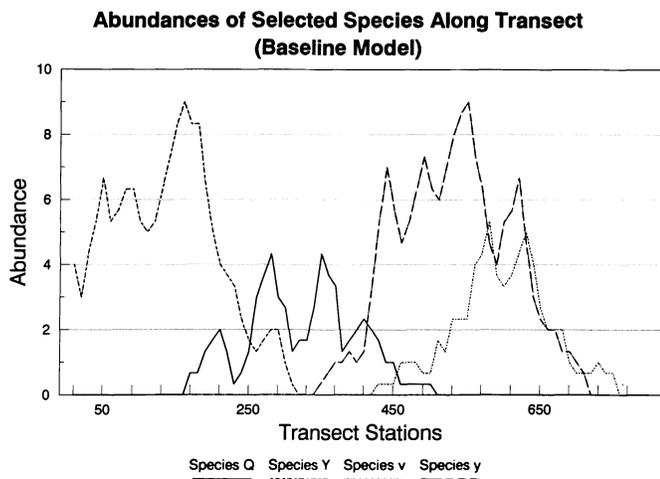


FIGURE 6—Abundance curves of four selected species along the 80-sample transect for the illustrated run of the basic model. Transect station numbers (x-axis) are the gradient coordinate values for the samples (abundance values are three-point moving averages).

ples definitively cluster most closely on the dendrogram with their nearest geographic neighbors.

Taken together, these attributes suggest that there is, indeed, a gradient in sample composition along the model transect, but the gradient is neither completely uniform nor continuous. In fact, at the level of individual clusters, sample compositions appear to vary randomly (see discussion of species covariance, below).

Given the well-known shortcomings of cluster analysis, the discontinuities on the dendrogram should not be taken at face value; this can be demonstrated using ordination. A detrended correspondence analysis (DECORANA) of the data is presented in Figure 8 (DECORANA is a particularly suitable ordination technique for the analysis of ecological data; see Hill and Gauch, 1980; Gauch, 1982). On this bivariate plot of sample scores for axes 1 and 2, samples belonging to each of the nine Q-mode clusters have been delineated. Clearly, transitions among cluster groupings are gradual; there is no evidence of the major discontinuities that were apparent on the dendrogram. At the same time, many of the essential attributes of the dendrogram are maintained in the ordination. There is very little spatial overlap among cluster-groups on the ordination, and the spatially systematic (with respect to the gradient) order of the groups in this objective analysis is the same as that depicted on the dendrogram. As was the case *within* clusters on the dendrogram, the ordering of samples within groups on the ordination is not spatially systematic. Thus, in this instance, where much of the variability in the data can be explained in a single dimension, cluster analysis and DECORANA provide comparable signals (although the ordination, of course, gives a more accurate rendering of the gradual transitions among samples). Moreover, as an exploratory technique for distinguishing between systematic and non-systematic

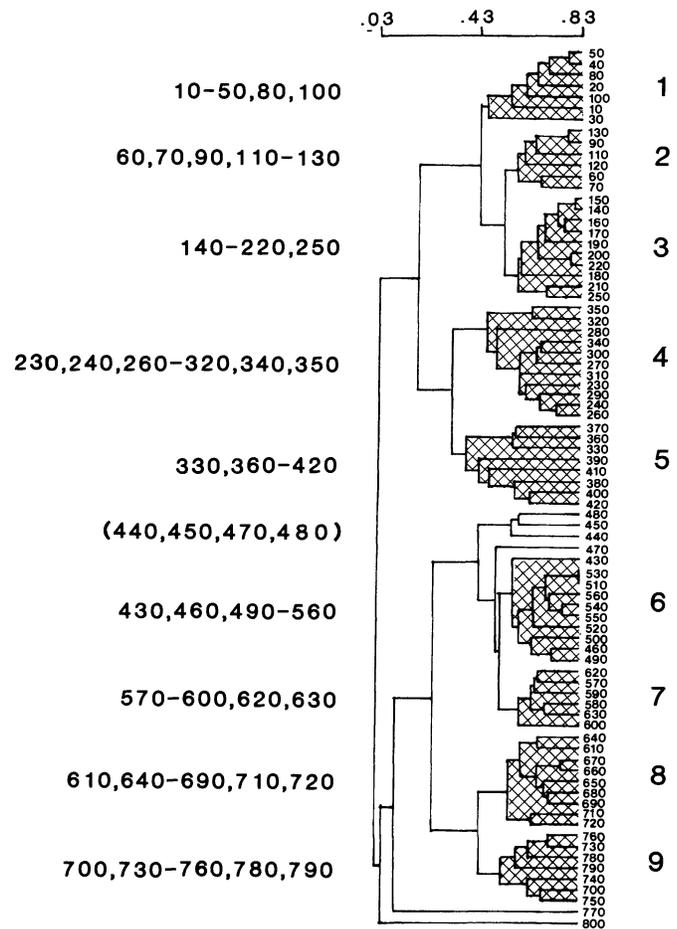


FIGURE 7—Q-mode cluster analysis of 80 samples from the illustrated basic run of the model (Unweighted Pair-Group Method with Arithmetic Averaging; percent transformation of samples; quantified Dice similarity coefficient; cophenetic correlation coefficient = 0.85). Sample labels are the gradient coordinate values; samples belonging to each cluster are summarized on the left. Note that the nine delineated clusters are cohesive and systematically ordered with respect to sample locations on the gradient. However, this ordering breaks down within clusters, suggesting a “stepped” gradient in faunal composition among samples (see text).

sample variability along the transect, cluster analysis is rather effective.

There is reason to believe that the kind of “stepped gradient” recognized here is characteristic, at some scale, of spatial faunal transitions in benthic marine systems. For example, Miller (1988) collected samples of accumulated molluscan skeletal remains at 10 m intervals on a 360 m transect in Smuggler’s Cove, St. Croix, U.S. Virgin Islands. Post-mortem transport was of only limited importance in this study area (see below), and there was a marked transition along the transect in the compositions of samples, associated with a measurable decrease in sea-grass cover. The dendrogram from a Q-mode cluster analysis of these data is presented in Figure 9; its primary

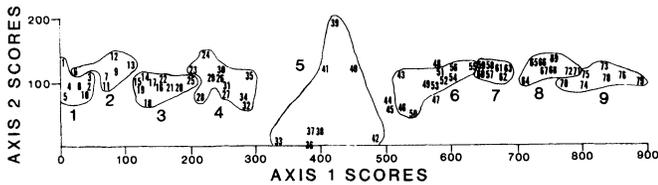


FIGURE 8—Bivariate scatter plot of sample scores for axes 1 and 2 of a detrended correspondence analysis carried out on 78 samples from the illustrated basic run of the model (samples 770 and 800 were outliers and, thus, were not included). Eigenvalues for axes 1 and 2 were, respectively, 0.928 and 0.134. For ease of plotting, the final digit of sample labels ('0') has been truncated.

attributes are strikingly similar to those exhibited by the model dendrogram (Fig. 7). There are six geographically cohesive clusters, ordered systematically with respect to their positions along the transect. However, there is little geographic ordering of samples within clusters. This is reflective of the discontinuous nature of lateral environmental transitions in the study area. Although seagrass cover generally decreased along the transect, there were regions, on the order of 50 to 100 m in length, where the amount of seagrass varied randomly rather than systematically. Lateral transitions in accumulated molluscan remains simply reflected these stepped environmental changes. As Miller (1988) noted, a more continuous decrease in seagrass cover, rather than the abrupt transitions that were measured, would probably have produced a more continuous transition in compositions of molluscan skeletal samples.

In describing communities, Whittaker (1975, p. 116) likened them to "colors man recognizes, and accepts as useful concepts, within the spectrum of wavelengths of light which are known to be continuous." Thus, Whittaker drew an analogy between a continuous spectrum and an environmental gradient. However, it is arguable that along any transect there must be a spatial level below which such an analogy breaks down; uniform, continuous transitions are probably rare on sea floors (see Springer and Miller, 1990). Barring substantial overprint of taphonomic processes, spatial patterns in accumulated skeletal elements along environmental gradients probably exhibit "nick-points," above which sample compositions vary systematically and below which they vary randomly.

Stability in Model Outcomes

The illustrated run of the basic model is not a unique solution. Because the model is dependent upon the selection of random numbers for the determination of species attributes and the placement of individuals on the coordinate grid, each run of the model will produce a different outcome. However, potential outcomes are constrained substantially by the design of the model. The basic model has been run and evaluated several times, and, while not identical, each outcome has produced a Q-mode dendrogram highly comparable to Figure 7. In all cases, the result

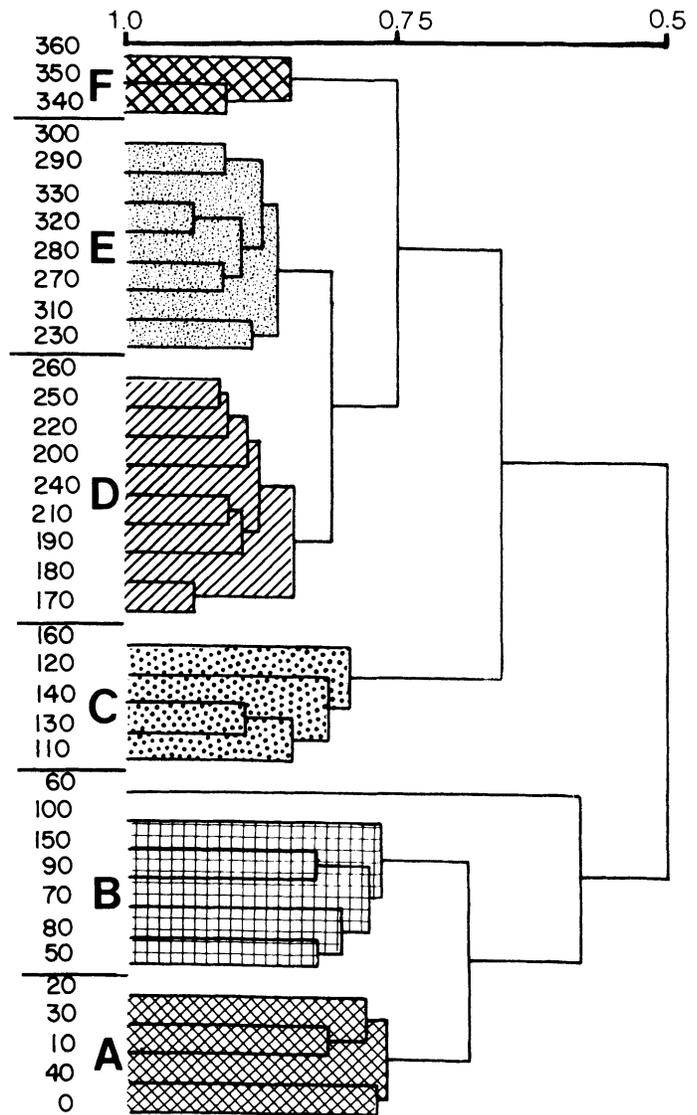


FIGURE 9—Q-mode cluster analysis of 37 subfossil molluscan samples from a transect in Smuggler's Cove, St. Croix, U.S. Virgin Islands. The sample labels represent the distances, in meters, from the south-eastern end of the transect. Note the comparability in dendrogram structure with Figure 7 (after Miller, 1988).

is a "stepped" gradient in faunal composition along the sample transect.

ASSESSMENT OF POST-MORTEM TRANSPORT

While the model appears to effectively simulate key attributes of benthic marine systems, the intention is not simply to provide such a replica. The potential power of this model is that it can be manipulated in various ways to test the effects of post-mortem processes on the compositions of resultant fossil assemblages. Here, we utilize

the model to test a proposed methodology for determining the amount of post-mortem transport in fossil assemblages along environmental gradients.

In the case of Smuggler's Cove, transport clearly has not been an important factor in the accumulation of molluscan skeletal remains along the 360 m transect. Had there been substantial post-mortem transport over distances in excess of 50 m, the result would have been a spatial distribution much less systematically related to environmental parameters than observed (Miller, 1988). However, it can still be asked whether there has been *any*, albeit limited, post-mortem transport. Miller (1989) speculated that minor transport, rather than localized random variability in environmental parameters, may have produced limited "smearing" of the overall gradient signal and, thus, the stepped pattern of sample variability observed on the Q-mode dendrogram (Fig. 9).

Species Covariance

Cummins et al. (1986a) proposed a methodology for statistically assessing the role of within-habitat, post-mortem transport in the formation of fossil assemblages. In brief, the method involves direct, pairwise comparisons of species distributions and is predicated on the observation that, within habitats, living individuals comprising a species are usually distributed randomly or contagiously (randomly distributed clumps) on a sea floor. Because of this tendency, it is unlikely that, in a suite of samples collected within a habitat, relative abundance patterns of any two species will be statistically similar (obvious exceptions would include instances of symbiotic or parasitic relationships between species). Barring post-mortem transport, relative abundances for skeletal accumulations of any two species should, likewise, not be comparable. However, if post-mortem transport takes place, the resultant sorting of skeletal material will produce within-habitat species distributions that are decidedly non-random and coincident. Because hydraulic sorting would potentially act in a similar fashion on many species, the expectation is that, following transport, relative abundance patterns of different species are more likely to be comparable.

Comparability of species abundance distributions has been termed *species covariance* (the term "covariance," as utilized here, is not to be confused with the formal usage of the term in statistics). Cummins et al. utilized the Spearman rank correlation coefficient to conduct pairwise comparisons of species abundances and, thus, statistically measure covariance. In a habitat where post-mortem transport has taken place, the expectation is that, for skeletal remains, a greater percentage of species will covary in abundance than would be expected by chance; the viability of this approach was demonstrated in a series of analyses conducted in two regions on the Texas Gulf Coast.

Cummins et al. recognized that other factors besides post-mortem transport can produce species covariance in skeletal accumulations. In the present context, the most important factor is environmental transition. With such transitions, species should covary in abundance (either

positively or negatively) because of their decidedly non-random preferences for particular environments. For example, when considering the Smuggler's Cove transect in its entirety, substantial species covariance exists because relative abundance patterns are intimately, and non-randomly, tied to transitions in the amount of seagrass cover.

Thus, covariance analysis can only be used to assess post-mortem transport if confined to a single habitat. However, this does not rule out the use of such a methodology for assessing the role of transport along environmental gradients. It would simply require that the gradient first be recognized and covariance analysis be limited spatially to regions where the environment varies only randomly (the individual "steps" on the gradient, alluded to previously). One potential approach would be to limit the scope of covariance analysis to groups of samples contained within discrete clusters, such as those in Figures 7 and 9, where it is evident that compositional variability among samples is not governed by the overall gradient.

The model can be used to test the feasibility of this methodology by first incorporating a limited amount of "post-mortem" transport into the design. Then, covariance patterns in Q-mode sample clusters for the untransported basic version can be compared to those for the transported version to assess directly the effects of small-scale transport on this metric.

Incorporation of Transport

Recognizing that transport necessarily involves sorting of skeletal elements (Cummins et al., 1986a), small-scale transport is incorporated by establishing a series of eight, evenly spaced, "depositional centers" along the modeled gradient (Fig. 10). When an individual is initially assigned to the coordinate grid in the basic model, it automatically falls under the auspices of the geographically closest depositional center. Then, it is reassigned (transported) to a new position along the gradient, based on the selection of a random number under the umbrella of a probability distribution that favors placement near its depositional center, as illustrated schematically in Figure 10.

The important aspect of reassignment, relative to initial assignment, is that *centers of gradient distribution* are no longer species specific. Rather, individuals are assigned new centers based simply on their initial location along the gradient. Moreover, the total number of centers is limited to eight, instead of, potentially, the initial 50 of the basic model. These attributes are in keeping with the observation that hydrodynamic factors involved in skeletal transport can act to produce the same geographic distribution regardless of species membership or the initial positions of individuals (Cummins et al., 1986a). In other words, resultant spatial patterns are dependent not so much on initial distributions as they are on physical processes that ultimately favor movement of material towards particular "collection zones."

The model incorporates eight depositional centers, rather than just a few or one, to reasonably simulate the probable upper limit of post-mortem transport in Smuggler's

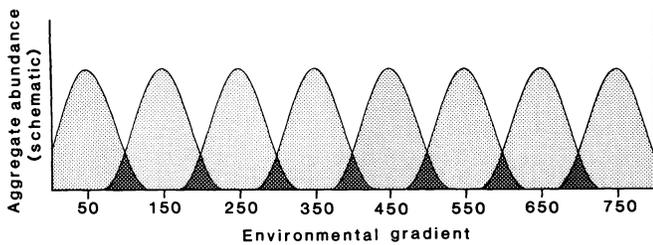


FIGURE 10—Schematic illustration of the incorporation of small-scale transport into the model. A series of eight, evenly-spaced, “depositional centers” is established; after their initial assignments to coordinate space, each individual falls under the auspices of the geographically nearest depositional center. Then, the individual is reassigned (transported) under the umbrella of a probability distribution that promotes placement of individuals near the depositional center (see text).

Cove (if there is transport at all). At most, an individual can be transported approximately 100 coordinate units along the modeled gradient. By contrast, if just one depositional center had been utilized, this would have permitted a scale of modeled transport far exceeding anything observed on the Smuggler’s Cove transect.

A final, but significant point about the incorporation of transport is that the model simultaneously keeps track of both the pre-transport and transported positions of all individuals. Thus, two modeled assemblages are generated: a transported assemblage and the corresponding assemblage that would have resulted had there been no transport. This permits direct measurement of the effects of transport (and, potentially, any other modeled taphonomic process). Obviously, this kind of comparison is impossible with real fossil or subfossil assemblages.

Comparison of Untransported and Transported Outcomes

Species Abundance Curves

Species abundance curves, following transport, for the four selected species illustrated earlier, are presented in Figure 11. In a gross sense, the four species occupy the same areas of the transect as before, but the role of transport is clearly visible here. Each species has several discrete peaks coinciding with the locations of modeled depositional centers. For example, species Q, v, and y all show local peaks in the vicinity of station 450.

Cluster Analysis of Transported Outcome

The dendrogram generated with Q-mode cluster analysis of the transported outcome is shown in Figure 12. Because it represents the transported version of the illustrated run evaluated earlier, this outcome can be compared directly with Figure 7.

The transported solution produces clusters that are geographically broader and less defined than the untransported outcome; several samples cannot be assigned definitively to a cluster (Fig. 12). Nevertheless, recognized

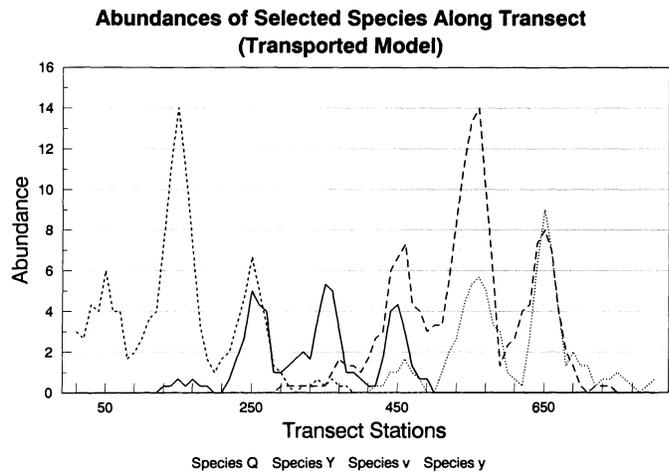


FIGURE 11—Abundance curves of four selected species along the 80-sample transect for the transported version of the illustrated model run. Note the abundance peaks in the vicinity of depositional centers (abundance values are three-point moving averages).

clusters are geographically cohesive, albeit encompassing larger geographic portions of the transect than clusters in the untransported solution. The ordering of clusters is geographically systematic, as it was before.

Thus, the effect of limited transport is to partly obscure, but by no means eliminate, the underlying gradient signal. Despite the broadening of sample clusters, the overall structure could still be described as a stepped gradient, and it is reasonable to ask whether the effects of transport could have been discerned had there not been a corresponding untransported solution with which to compare it.

Within-Cluster Species Covariance

Among samples from each of the nine Q-mode clusters generated in the untransported solution (Fig. 7), relative abundances for all possible pairs of species present were compared using the Spearman rank correlation coefficient as the measure of species covariance (see above). The percentages of species comparisons in each cluster that showed significant covariance are presented in Table 3. They ranged from 4 to 12 and averaged 9.1; clearly, there was no more species covariance within clusters than the 10% expected by chance at $\alpha = 0.10$. Results for the same kind of analysis of the transported solution are shown in Table 4. In this case, the four percentages ranged from 17 to 41 and averaged 25, well above levels expected by chance.

Therefore, the role of transport is clearly discernible by evaluating species covariance within sample clusters. In the case where there was, by design, no transport (the basic model), covariance values did not exceed those expected by chance. However, when transport was included, even on the limited scale incorporated here, within-cluster species covariance increased measurably.

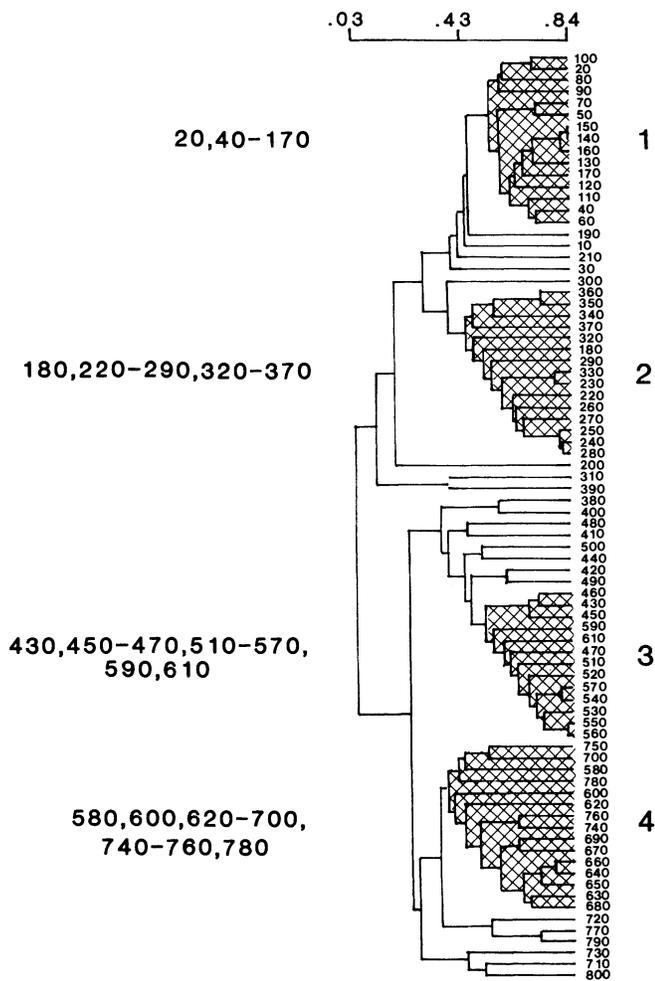


FIGURE 12—Q-mode cluster analysis of the 80 samples from the transported version of the illustrated model run (Unweighted Pair-Group Method with Arithmetic Averaging; percent transformation of samples; quantified Dice similarity coefficient; cophenetic correlation coefficient = 0.88). Geographically, the clusters are broader and less well-defined than the untransported version. However, clusters are relatively cohesive and the ordering of clusters is geographically systematic.

Smuggler’s Cove Species Covariance

The effectiveness of within-cluster covariance analysis for diagnosing transport in the model suggests that this methodology might be viable for discerning transport, if it has taken place, within habitats along an environmental gradient. As a test of this methodology on real data, species covariance analysis was applied to five of the six sample clusters from the Q-mode analysis of the Smuggler’s Cove data (Fig. 9; cluster F could not be used because it contained an insufficient number of samples). The results, presented in Table 5, are striking and point to the potential power of this technique. Clusters A and B show covariance at about the level expected by chance, whereas clusters C, D, and E all exceed this level substantially. This dichotomy

TABLE 3—Percentage of species pairs showing significant covariance ($\alpha = 0.10$) within clusters of the untransported model solution.

| Cluster | Number of samples | Percent significant |
|---------|-------------------|---------------------|
| 1 | 7 | 10 |
| 2 | 6 | 6 |
| 3 | 10 | 10 |
| 4 | 11 | 11 |
| 5 | 8 | 8 |
| 6 | 10 | 11 |
| 7 | 6 | 4 |
| 8 | 9 | 12 |
| 9 | 7 | 10 |
| Mean: | | 9.1 |

TABLE 4—Percentage of species pairs showing significant covariance ($\alpha = 0.10$) within clusters of the transported model solution.

| Cluster | Number of samples | Percent significant |
|---------|-------------------|---------------------|
| 1 | 15 | 41 |
| 2 | 15 | 19 |
| 3 | 13 | 17 |
| 4 | 15 | 23 |
| Mean: | | 25.0 |

suggests that there has, indeed, been limited transport along one portion of the transect, but no transport (down to the 10 m lateral scale of sampling) along the other portion.

Miller (1988) showed that the part of the study area encompassing samples from clusters A and B (the southern portion of the transect) was carpeted with seagrass (dominated by *Thalassia*), whereas seagrass cover was substantially less dense on the remainder of the transect (Fig. 13). The spatial coincidence of the southward increase in seagrass density and the decline in apparent skeletal transport appears to be a manifestation of the well-known ability of dense seagrass cover to reduce bottom energy (Ginsburg and Lowenstam, 1958; Scoffin, 1970). In an area like Smuggler’s Cove, where wave and current action is minimal in the first place (Miller, 1988), the effect of seagrass must be to reduce ambient benthic energy levels to near zero, thus precluding substantial transport. Outside the zone of dense seagrass, there is sufficient energy (perhaps during storms) to have effected small-scale transport on the order of a few tens of meters or less. Clearly, transport has not exceeded 40–50 m even outside the seagrass beds, or the observed clustering pattern (Fig. 9) would have been disrupted.

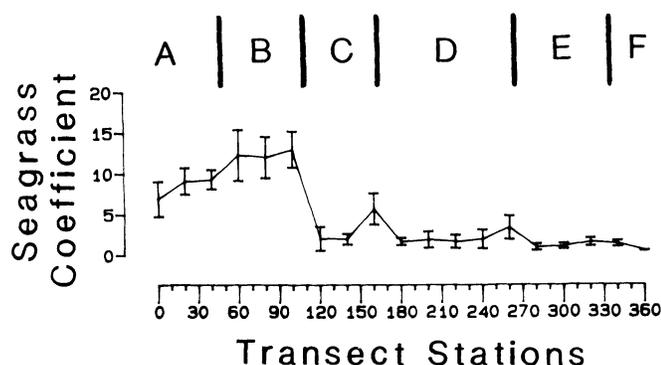


FIGURE 13—Graph depicting transitions in the amount of seagrass cover along the transect in Smuggler's Cove, summarized with a "seagrass coefficient" (see Miller, 1988); geographic zones of Q-mode clusters (Fig. 8) have been denoted (lettered A through F across the top). There is a substantial transition in seagrass cover between stations 100 and 120, which corresponds spatially with a transition in within-cluster species covariance (after Miller, 1988).

DISCUSSION

Estimating Post-Mortem Transport

Beginning with the earliest discussions of taphonomy (e.g., Da Vinci, reprinted in Mather and Mason, 1939; Boucot, 1953), the issue of post-mortem skeletal transport has been a central concern in paleontology. For the most part, this has been one component of a more general effort to determine whether fossil assemblages can reasonably reflect the living faunas from which they were derived. In attempting to identify faunal elements as exotic or indigenous, several previous taphonomic studies have been well-suited for this general goal (e.g., Johnson, 1960, 1965; Chave, 1964; Lawrence, 1968; Warne, 1969, 1971; Schafer, 1972; MacDonald, 1976; Peterson, 1976; Stanton, 1976; Warne et al., 1976; Bosence, 1979; Fürsich and Flessa, 1987).

However, many investigations, across the spectrum of paleontology, would benefit from more precise determination of the *degree* to which skeletal material has been transported. In the context of spatial variability in the fossil record, a primary goal should be to distinguish definitively between a meaningful biological signal and noise induced by post-mortem processes. To this end, recent comparative analyses of taphonomic effects (the "taphofacies" approach; e.g., Brett and Baird, 1986; Speyer and Brett, 1986, 1988; Parsons et al., 1988; Davies et al., 1989; Meyer et al., 1989) have provided fresh insight and a promising framework for determining *relative* degrees of transport in fossil assemblages. However, it was not the intent of these studies to provide determinations of the *absolute* extent of transport.

The methodology proposed here represents a general framework for estimating the absolute amount of skeletal transport in any fossil assemblage; it should be as readily applicable to Ordovician brachiopod assemblages in Cincinnati as it was to Recent molluscan assemblages in St. Croix. To be successfully conducted, the primary require-

TABLE 5—Percentage of species pairs showing significant covariance ($\alpha = 0.10$) within clusters of samples from Smuggler's Cove, St. Croix.

| Cluster | Number of samples | Percent significant |
|---------|-------------------|---------------------|
| A | 5 | 11 |
| B | 6 | 11 |
| C | 5 | 33 |
| D | 9 | 31 |
| E | 8 | 21 |

ments are: 1) a spatially systematic sampling program, preferably including outcrop-scale collection of samples at confined lateral intervals along individual bedding planes; and 2) the collection of relative abundance data for sampled taxa. These sampling attributes permit the application of multivariate techniques to discern the overprint of faunal gradients and delineate habitats. Then, within-habitat species covariance analysis can be applied to directly diagnose transport.

Utility of the Numerical Model

The utility of the numerical model in testing effects of transport points to its suitability and potential power as a tool in the evaluation of taphonomic processes. Because of the three-dimensional structure of the model, as well as the incorporation of multiple habitats along a gradient, future applications of the model can include further analysis of transport, as well as evaluation of other taphonomic effects. Specifically, the model will permit analysis of: 1) differential transport as a function of position on the modeled gradient to evaluate onshore-offshore proximity effects (see Aigner, 1979, 1980, 1985); 2) differential transport as a function of ecological tier (see earlier discussion); 3) differential transport as a function of shell size; 4) incorporation of dissolution "indices" to estimate the effects of differential dissolution overprints on resultant assemblages; 5) incorporation of temporal environmental transitions to further explore the question of time-averaging.

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