Lateral Mixing and Spatial Resolution in Molluscan Assemblages of Smuggler's Cove, St. Croix, U.S.V.I.

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INTRODUCTION

Paleoecological and evolutionary investigations commonly involve assessments of spatial and temporal faunal trends in preserved fossil assemblages. However, the compositions and distributions of benthic marine faunal assemblages are subject to a variety of physical and chemical processes that can substantially alter even the most readily preservable organisms (see, for example, Boucot, 1953; Johnson, 1960; Kornicker *et al.,* 1963; Chave, 1964; Driscoll, 1970; Clifton, 1971; Boyd and Newell, 1972; Schopf, 1978; Brett and Baird, 1986). Thus, any evaluation of the significance of a particular fossil assemblage must necessarily involve consideration of the post-mortem processes involved in its formation. The study of such processes is known as taphonomy.

Until recently, taphonomic studies were generally limited to evaluations of information loss from fossil assemblages (e.g. Lawrence, 1968). However, it is now clear that there are important diagnostic aspects to taphonomy, with potential utility for resolving paleontological and sedimentological problems (Kidwell, 1986; Brett and Baird, 1986; Parsons *et al.,* 1988). For example, distributional and preservational aspects of fossil assemblages may themselves be diagnostic of particular depositional regimes, thereby aiding substantially in paleoenvironmental reconstruction (e.g. Norris, 1986; Speyer and Brett, 1986; Fursich and Flessa, 1987; Staff and Powell 1988).

The emergence of taphonomic principles as diagnostic tools in geology is dependent on the development of rigorous, quantitatively-based guidelines that can be directly applied to the fossil record. The purpose of this paper is to briefly summarize the results of a study conducted in Smuggler's Cove that is part of an ongoing effort to establish such guidelines. This paper focuses on lateral mixing and its impact on spatial resolution in accumulating fossil assemblages. The following paper by Parsons, deals with the post-mortem physical deterioration of skeletal material. Studies of physical deterioration enhance the possibility of accurately determining depositional conditions within preserved ancient environments, while evaluations of lateral mixing and spatial resolution in the same habitats provide a basis in the fossil record for distinguishing between biologically meaningful patterns of faunal distribution, and those associated with post-mortem transport (see also Cummins *et al.,* 1986).

BACKGROUND

In the past decade, the systematic evaluation of spatial transitions in "soft-bottom" fossil assemblages, commonly referred to as "gradient analysis", has emerged as a valuable investigative tool in paleoecology and evolutionary paleobiology (e.g. Cisne and Rabe, 1978; Cisne *et al.,* 1982a,b; Cisne and Chandlee, 1982; Springer and Bambach, 1985). As a consequence of such analyses, we have developed an improved understanding of the spatial persistence, or the lack thereof, of faunal assemblages along paleoenvironmental gradients. However, to date, most analyses of spatial variability in fossil assemblages have not involved detailed lateral sampling along bedding planes at individual outcrops. Rather, spatial variability and gradients are generally assessed on the basis of faunal transitions from outcrop to outcrop, sometimes with a spacing of several tens of kilometers between lateral samples. While this wide spacing does not invalidate the results of such studies, it is evident that smaller scales of spatial variability have been overlooked.

Clearly, lateral post-mortem transport of skeletal material is limited to some degree; large-scale faunal gradients would not otherwise be recognizable in the fossil record. Even in the case of storm-deposition, fossil transport may not be pronounced in at least some instances (see Kreisa, 1981; Aigner, 1979,1980; Aigner and Reineck, 1982). Nevertheless, it has been assumed implicitly that, on the scale of a single outcrop (a hundred meters or less), biologically meaningful spatial patterns are generally obscured because of post-mortem processes.

The primary objective of the Smuggler's Cove study was to determine the degree to which environmental changes on a relatively confined spatial scale are reflected by lateral transitions in accumulating molluscan skeletal remains. Utilizing 37 faunal samples, collected at 10 m lateral intervals along a 360 m transect, non-systematic spatial variability within the death assemblage was

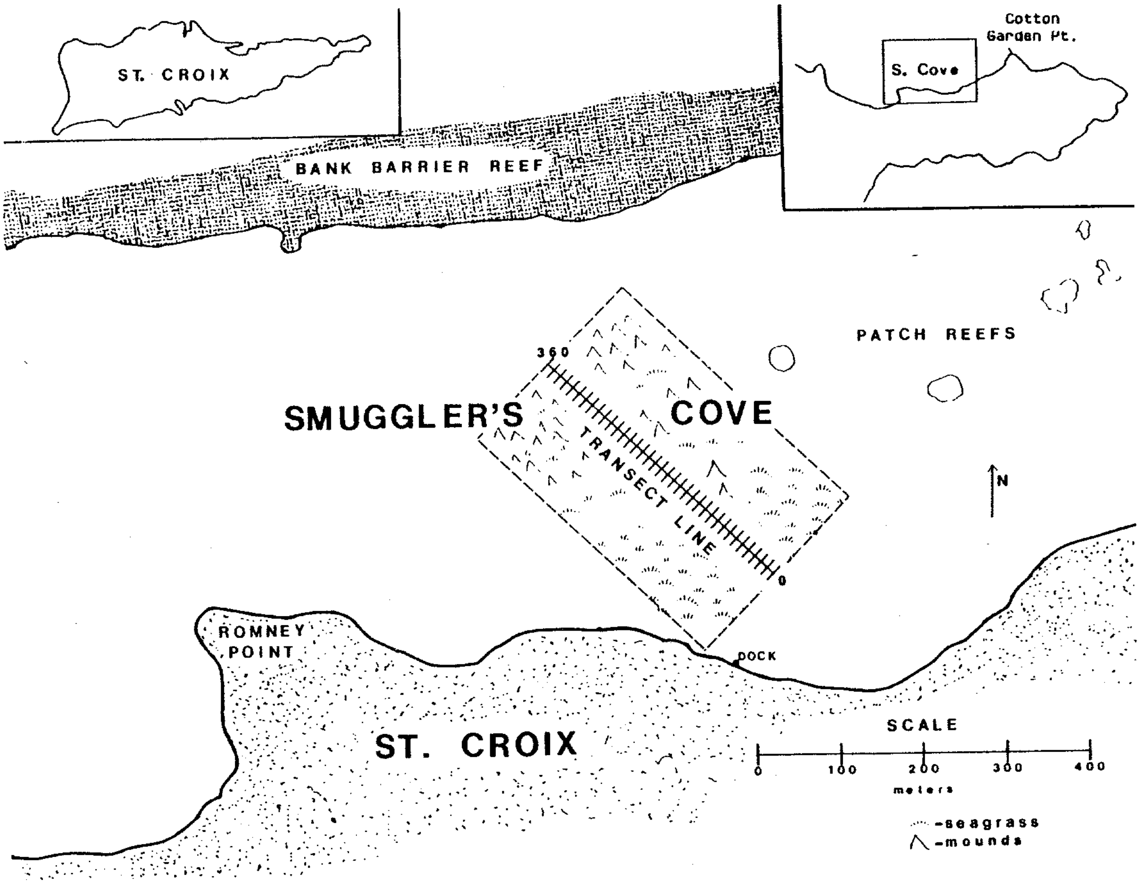

Figure 1. Map of the study area. In the area of the transect line, there is *a northwestward decrease in seagrass cover and increase in the concentration of mounds built by the burrowing shrimp,* Callianassa. *Left inset: The island of St. Croix. Right inset: The eastern end of the island From Miller (1988).*

distinguished from systematic faunal differences associated with environmental change. This permitted development of a baseline estimate of the degree to which molluscan skeletal material has been transported within the study area.

ENVIRONMENTAL PARAMETERS AND METHODOLOGY

Methodology for this analysis is discussed in detail by Miller (1988); it will be summarized only briefly here. The 360-m sampling transect extended from an area of dense benthic vegetation (including seagrass and macroalgae) at its southeastern end, to a highly bioturbated zone, with no vegetation, at the northwestern end (Fig. 1). The central region of the transect was intermediate in character between these two extremes; vegetation was present, but at densities less than the southeastern end. There was a fairly continuous increase in water depth along the transect from 3 m in the southeast to 6 m in the northwest (Fig. 2A; see caption for explanation of station numbers).

Samples of accumulated molluscan skeletal material were collected at 10 m lateral intervals along the transect using a core tube and a SCUBA-powered airlift. In all cases, the volume of material sampled was equivalent; only the fraction greater than 4 mm in size was retained for further analysis. In the laboratory, molluscan skeletal material from each sample was identified to species-level, when possible, and counted. The resulting matrix of species abundance data was subjected to multivariate analysis (see below) to help interpret patterns of faunal variability among the samples. For the same purpose, several environmental attributes, including water depth and degree of vegetation cover, as well as mean grain size, sorting, and silt/clay percentages of bottom sediments, were measured throughout the study area. These data are summarized in Figure 2.

Density of seagrass cover, as measured by bottom censusing at 20-m intervals along the transect, was summarized by a "seagrass coefficient" (Fig. 2B; see Miller, 1988 for details). There was a substantial decrease in seagrass cover between stations 100 and 120, and a smaller, but noticeable transition to even lower coefficient values between stations 260 and 280; there was no seagrass cover at station 360. Sediment patterns depicted in Figure 2C and 2D do not suggest a northwestward tendency towards increased grain size, even though such an increase might be expected given the decreasing seagrass density in that direction (see Ginsburg and Lowenstam, 1958; Scoffin, 1970).

RESULTS

The data matrix of molluscan skeletal remains was evaluated using two-way cluster analysis (Fig. 3); details of this methodology are provided in Miller (1988) and references cited therein. The technique involves construction of graphical tree diagrams, known as dendrograms, based on the relative similarity of samples with respect to their species composition (Q-mode analysis) and the relative similarity of species with respect to their distributions among samples (R-mode analysis). Proximities of samples or species on a dendrogram reflect their similarities to one another, as calculated with a numerical coefficient (see Miller, 1988).

Of particular note in the Q-mode analysis is the close relationship between sample locations on the dendrogram and their geographic positions along the transect. Cluster A contains all the samples from stations 0 through 40, and the other five clusters are similarly geographically cohesive. This is best illustrated in Figure 4, where sample stations along the transect have been shaded with patterns that correspond to their positions within the six Q-mode clusters (Fig. 3). Only three of the 37 samples are "out of place" (samples 60, 150, and 230). Sample 60 was not assigned to any of the six clusters, while sample 150 was contained in cluster B and sample 230 was located in cluster E.

Thus, the Q-mode dendrogram displays an underlying pattern of pronounced, systematic transition in the faunal compositions of samples along the transect. The R-mode dendrogram and the dot-grid that comprise the remainder of the two-way analysis (Fig. 3) provide insight into the details of these transitions. In the R-mode analysis, only the 32 most abundant species were included; these species accounted for more than 90% of collected specimens. The R-mode dendrogram shows three major clusters of species that contain all but five of the species included in the analysis. On the accompanying grid, a dot was placed at the point of intersection of a species and sample whenever the abundance of the species in that sample exceeded a minimum threshold value (see Miller, 1988); sizes of the dots reflect relative abundance values.

The dot grid reveals that samples from the southeastern end of the transect, in Q-mode clusters A and B, are dominated by species from R-mode clusters I and II. In samples from Q-mode cluster A, species from R-mode cluster I are somewhat more abundant than those from R-mode cluster II, whereas the opposite appears to be the case among samples from Q-mode cluster B. In Q-mode clusters D, E, and F, which contain samples from the northwestern portion of the transect, faunal elements from R-mode cluster III are most abundant. Samples in Q-mode cluster C, from the central area of the transect, are intermediate in faunal composition, containing particularly high abundances of species from R-mode clusters II and III.

Thus, along the transect, there is a pronounced southeast-to-northwest faunal transition in molluscan skeletal remains from species of R-mode clusters I and II to those of cluster III. On the basis of life habits of the constituent species, it can be readily demonstrated that these faunal changes are associated with the principal environmental transition along the transect: the northwestward decrease in seagrass cover (Fig. 2B). Most of the abundant species in R-mode clusters I and II are gastropods known to live epifaunally on seagrass blades, and lucinid bivalves documented to be among the principal infaunal occupants of seagrass-covered bottoms (Miller, 1988). It is not surprising that these species dominate the southeastern portion of the transect (Q-mode clusters A and B), where seagrass cover is rather dense. Towards the northwestern end, seagrass cover becomes lighter, and

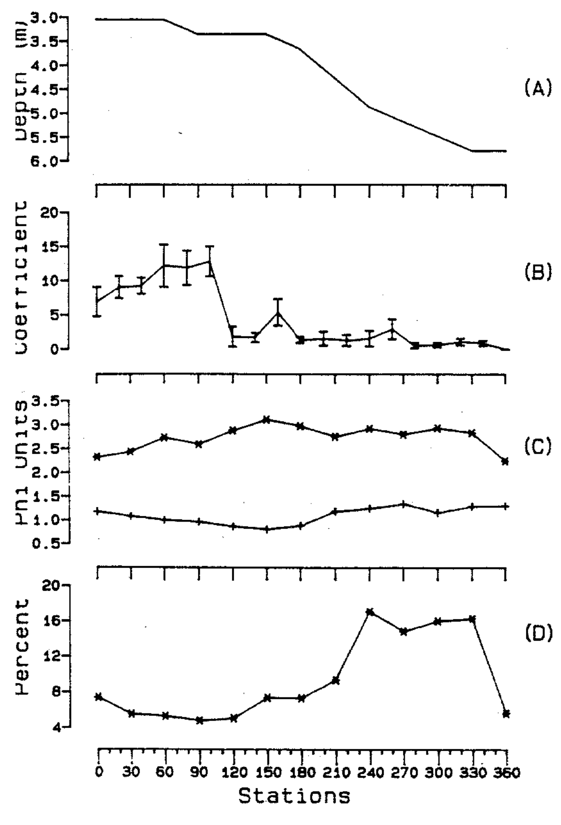

Figure 2. *Graphs of environmental attributes along the transect. Station numbers in the figure and throughout the paper represent distances in meters, from the southeastern end of the transect. A = water depth; B = seagrass density (the "seagrass coefficient"), C = mean grain size (top curve) and sorting (inclusive graphic standard deviation; bottom curve) of bottom sediments. From Miller (1988).*

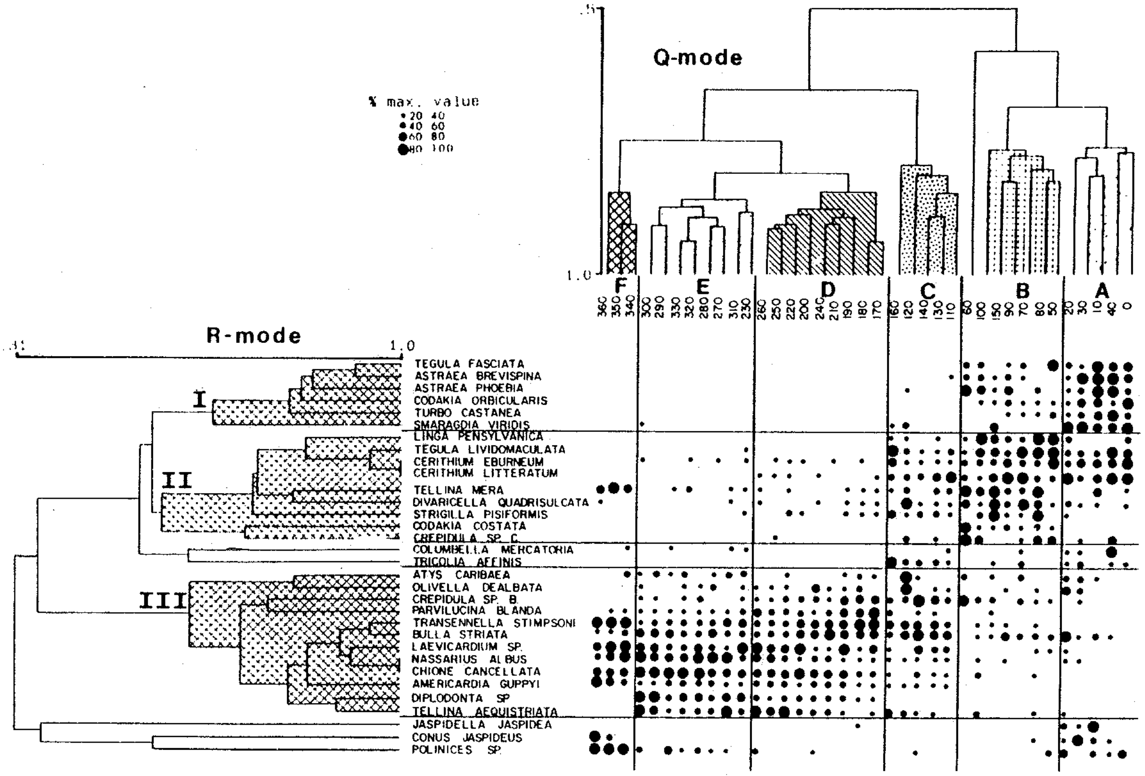

Figure 3. *Two-way cluster analysis of the 37 molluscan samples collected along the transect. For explanation of dot grid and interpretation, see text. A series of horizontal and vertical lines is placed on the grid to reflect the clustering patterns seen in each dendrogram. From Miller (1988).*

there is a corresponding shift among accumulated molluscs to R-mode cluster III faunal elements, dominated by free-burrowing bivalves and sand-dwelling gastropods. Epifaunal gastropods become considerably less abundant towards the northwest because of the limited seagrass surface area for potential attachment.

The relationship between species abundances and seagrass density is further attested to with correlation analysis. The abundances of most species in R-mode clusters I and II are positively correlated along the transect with corresponding values of the seagrass coefficient, while there are negative correlations between seagrass-coefficient values and abundances of most species in R-mode-mode cluster III. The majority of these positive and negative correlations are statistically significant at the 99.9% level (Miller, 1988).

DISCUSSION

While it is conceivable that some form of hydraulic sorting is capable of producing the faunal transitions recognized here, the documented association between molluscan life habits and seagrass cover indicates that this is a remote possibility at best. It is evident that faunal transitions do not result from post-mortem transport.

However, transport might play a limited role in producing observed faunal distributions. Whereas Q-mode cluster analysis (and other multivariate techniques; see Miller, 1988) reveals a systematic geographic ordering of the six sample clusters associated with the underlying faunal transitions, the ordering of samples within each cluster is not nearly so systematic. There are two potential explanations for these non-systematic arrangements:

1) The non-uniform decrease in seagrass cover--Although seagrass cover decreases along the transect, this transition is neither continuous nor gradual. As noted earlier, there was a marked decline in the seagrass coefficient between stations 100 and 120, and a smaller decline between stations 260 and 280. These declines correspond closely with clustering patterns on the Q-mode dendrogram. There is a break between the branch containing clusters A and B and that containing the remaining clusters, corresponding to the major seagrass decline; the break between clusters D and E appears to coincide with the smaller decrease. However, there were zones of nearly uniform seagrass density extending for 60 m or more along the transect. The nonsystematic ordering of faunal samples within clusters may simply reflect random variability in living molluscan assemblages at this limited spatial scale, associated with uniform, or randomly varying, seagrass cover.

2) Minor post-mortem transport--Smuggler's Cove is a well-protected backreef lagoon, with limited wave and

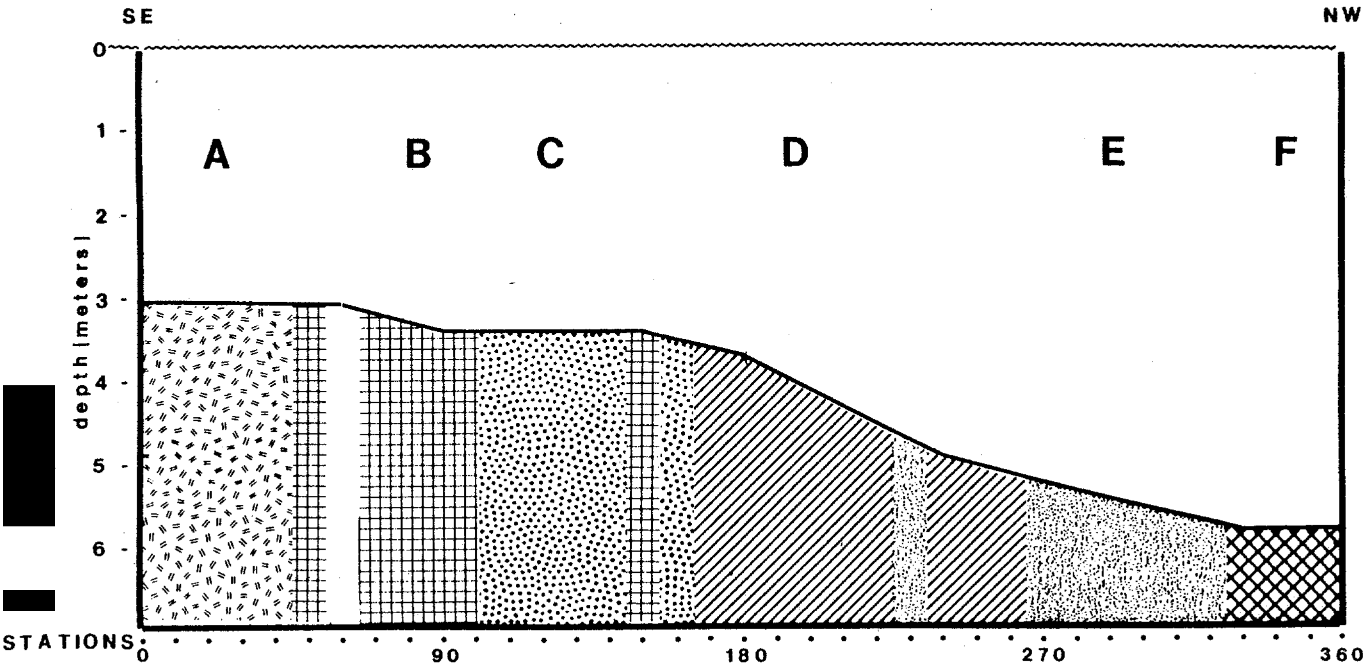

Figure 4. *Depth profile of the transect, with shading patterns corresponding to Q-mode clusters (Fig. 3) superimposed at individual stations to illustrate the geographic cohesiveness of the clusters.*

current activity (Miller, 1988). It is difficult to imagine that there would be significant fair-weather transport of skeletal material, except for minor movement as a consequence of bioturbation by the burrowing shrimp, *Callianassa.* However, during major storms, limited lateral transport might take place. It is possible that small-scale random variability may have resulted from storm transport, the effects of which might also be minor relative to that in other areas, because of the protected setting of the study area.

In any case, it is clear that post-mortem transport is no more than a minor factor in Smuggler's Cove. The data indicate that, at most, skeletal material is transported a few tens of meters. With respect to the fossil record, this suggests that biologically meaningful spatial variability is potentially preservable on a similarly small scale along individual bedding planes. However, it is arguable that much of the fossil record consists of assemblages deposited in higher energy conditions on continental shelves and in epicontinental seas. To calibrate the potential lateral resolving power of the fossil record, it will ultimately be useful to conduct analyses comparable to the Smuggler's Cove study in a variety of depositional settings subject to differing levels of benthic disturbance.

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