

REWORKING DIVERSITY: EFFECTS OF STORM DEPOSITION ON EVENNESS AND SAMPLED RICHNESS, ORDOVICIAN OF THE BASIN AND RANGE, UTAH AND NEVADA, USA

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ABSTRACT

Storm-generated event beds are an important source of paleoecological information, especially in Paleozoic strata. Storm deposition and subsequent physical and biological modification can potentially alter the diversity structure of death assemblages significantly. To examine the effects of storm deposition on fossil assemblage composition, storm beds are compared with co-occurring beds representing background sedimentation in 67 samples from six Ordovician mixed carbonate-clastic units deposited above the maximum storm wave base. In the great majority of pairwise comparisons, evenness and sampled richness are higher in storm beds than in background beds. This effect is not explained by differences in lithification, skeletal fragmentation, or in the proportions of aragonitic or multielement skeletons. The elevated diversity of storm beds can result from homogenization of fine-scale faunal patchiness preserved in background beds or may be due to taphonomic feedback. The relative importance of these two end-member scenarios can be evaluated with detrended correspondence analysis. In shallow, carbonate-dominated environments, the former appears to predominate, while the latter is more important in a deeper setting dominated by fine-grained clastics. The disparity between background beds and storm beds suggests that, at least in the Lower Paleozoic, background beds may record a higher-resolution paleoecological signal while storm beds record a more complete census of alpha diversity. Because post-Middle Ordovician increases in the depth and intensity of bioturbation may have diminished the temporal resolution and increase the faunal completeness of background beds, this disparity is not necessarily expected in younger strata.

INTRODUCTION

Storm-generated bioclastic event beds are a conspicuous and much-studied feature of the stratigraphic record (Einsele and Seilacher, 1982; Aigner, 1985; Kidwell and Aigner, 1985; Kidwell, 1986a; Einsele et al., 1991; Copper, 1997; Li and Droser, 1997, 1999; Miller, 1997; McFarland et al., 1999; Boyer and Droser, 2003). Through winnowing of fine sediments deposited during intervals of background sedimentation, storm-associated waves and currents create beds composed largely of bioclasts and coarse sediments (Seilacher and Aigner, 1991). This process can affect the structure of fossil assemblages in many ways. Large storms can degrade both spatial and temporal resolution by eroding and redepositing previously accumulated sediments, mixing the remains of organisms that did not live in the same time or place (Kreisa and Bambach, 1982; Sadler, 1993). High-energy events can sort bioclasts by shape and size (Menard and Boucot, 1951; Westrop, 1986; Lask, 1993; Prager et al., 1996; Martin, 1999) and may selectively destroy fragile shells (Kowalewski, 1996; Kowalewski and Flessa, 1996). By altering porosity and bulk sediment composition, storms can influence pore-water chemistry and hence shell dis-

solution (Best and Kidwell, 2000; Best et al., 2001). Following initial deposition, storm beds may experience early cementation, creating substrate conditions favorable for colonization by encrusting taxa that were previously excluded from the site (Kidwell and Jablonski, 1983; Kidwell, 1986b; Walker and Diehl, 1986).

Delineating within-habitat (alpha) diversity patterns through time has been a major research program in paleobiology (Bambach, 1977; Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985; Sepkoski, 1988; Westrop and Adrain, 1998; Adrain et al., 2000; Alroy, 2003; Bush and Bambach, 2004; Peters, 2004a, 2004b). In many such studies, a few samples are taken to represent alpha diversity for an entire depositional environment or time interval. Because many fossils can be retrieved from relatively small bulk samples of bioclastic storm beds, they are attractive targets for sampling and are disproportionately represented in paleontological collections. This is especially true in the tropical carbonate and mixed carbonate-clastic depositional systems that constitute much of the sedimentary record (Marsaglia and Klein, 1983; Brandt, 1986; Bush and Bambach, 2004). For example, although most level-bottom carbonate sequences are volumetrically dominated by mudstones and wackestones (Demico and Hardie, 1994), packstones and grainstones, many of which are storm generated, constitute 45% of all Lower Paleozoic carbonate collections in the Paleobiology Database (<http://paleodb.org/cgi-bin/bridge.pl>, summary table generated 1/31/07), which are classified according to Dunham's (1962) carbonate classification scheme. Due presumably to the net drift of continental landmass to higher latitudes and the consequent decline in representation of tropical environments between the Paleozoic and Cenozoic (Allison and Briggs, 1993; Walker et al., 2002), there is also a strong temporal trend in the proportional representation of packstones and grainstones among all paleontological collections (Fig. 1). Because of these environmental and temporal biases in their distribution, it is important to understand the ways in which the diversity structure of storm-generated beds may be modified relative to beds representing background sedimentation in the same depositional environments.

This study compares the diversity structure and faunal composition of storm beds and background beds using a data set of 67 macrofaunal collections from six Lower and Middle Ordovician mixed carbonate-clastic stratigraphic units in the Basin and Range Province (Utah and Nevada). Though these samples represent only a limited environmental and temporal gradient, they offer an opportunity to make direct within-habitat comparisons without the numerous complications that would be involved in a broader-scale analysis, and the sampled units are in many ways typical of tropical Paleozoic depositional environments.

GEOLOGICAL SETTING

Ordovician rocks outcrop in a broad SW–NE belt across the Basin and Range region of Utah and Nevada (Fig. 2A). They are particularly well exposed and richly fossiliferous in the Ibex area of western Utah (Hintze, 1952; Fortey and Droser, 1996; Ross et al., 1997) and in the Antelope Valley area of central Nevada (Ross, 1970; Ross et al., 1991; Fortey and

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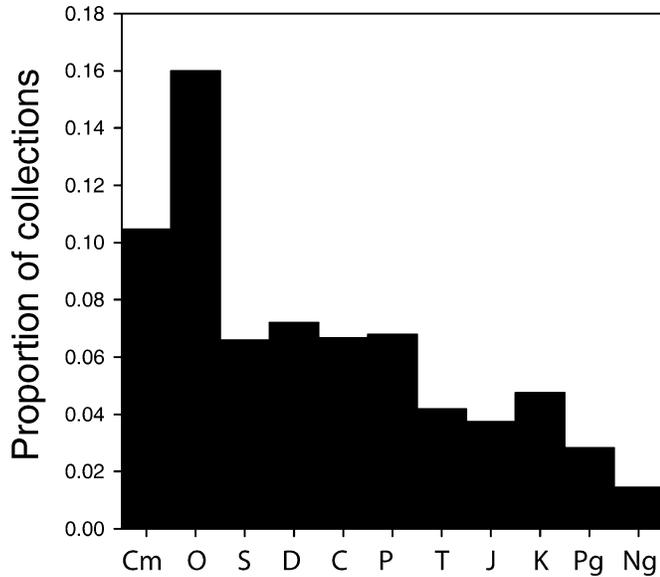


FIGURE 1—Proportional representation of packstones and grainstones through time in the 26,166 marine invertebrate collections in the Paleobiology Database (<http://paleodb.org/cgi-bin/bridge.pl>, summary table generated 1/31/07) that include well-resolved lithological information.

Droser, 1999). Early Ordovician Ibx Series strata were deposited on a broad, shallow, mixed carbonate-clastic ramp lying near the equator (Ross, 1977; Ross et al., 1989). Middle Ordovician Whiterock Series strata record the development of a carbonate platform rimmed by oncolite shoals, which continued to receive considerable clastic input (Ross et al., 1989).

In the Ibx area and correlative sections in the nearby Thomas Range, upper Ibx series and lower Whiterock series strata consist of massive to medium-bedded carbonates interbedded at decimeter-to-meter scales with shales and bioturbated mudstones (Hintze, 1952, 1973; Ross et al., 1997). Shallow subtidal aggradational parasequences dominate the Ibxian upper Fillmore and Wah Wah Formations and the Whiterockian Juab Limestone (Dattilo, 1993, Finnegan and Droser, 2005). Above these units, the shale-dominated facies of the lower Kanosh Formation record local deepening and periodically oxygen-restricted conditions, possibly related to the formation of shelf-edge oncolite buildups to the west (McDowell, 1987; Ross et al., 1989; Boyer and Droser, 2003). In the Antelope Valley area, the Ninemile Formation and Antelope Valley Limestone record generally more distal, midshelf open-water depositional environments.

Owing to its tropical position, the shelf was regularly swept by storms, and storm-generated event beds are conspicuous throughout the Ibx and Whiterock series (Fig. 3; Dattilo, 1993; Li and Droser, 1999). Such beds can be recognized by a suite of features (Seilacher and Aigner, 1991). They generally have uneven and scoured contacts with underlying beds, are composed largely of highly fragmented shell material and intraclasts, and, especially in more distal environments, are often capped by mega-ripple sets. Though individual storm beds are rarely more than 15 cm thick, in proximal facies amalgamated grainstones recording multiple reworking events are common and can be more than 50 cm thick (Li and Droser, 1999). Because skeletal remains in such beds are usually extremely fragmented and abraded to the point that even family-level identification is difficult, they were not sampled for this study.

METHODS

All samples analyzed in this study come from single beds <30 cm thick and were collected by one of us (SF) between 2001 and 2004. Storm beds were selected based on the criteria outlined above. Because storm activity can also result in burial without significant reworking (Seilacher

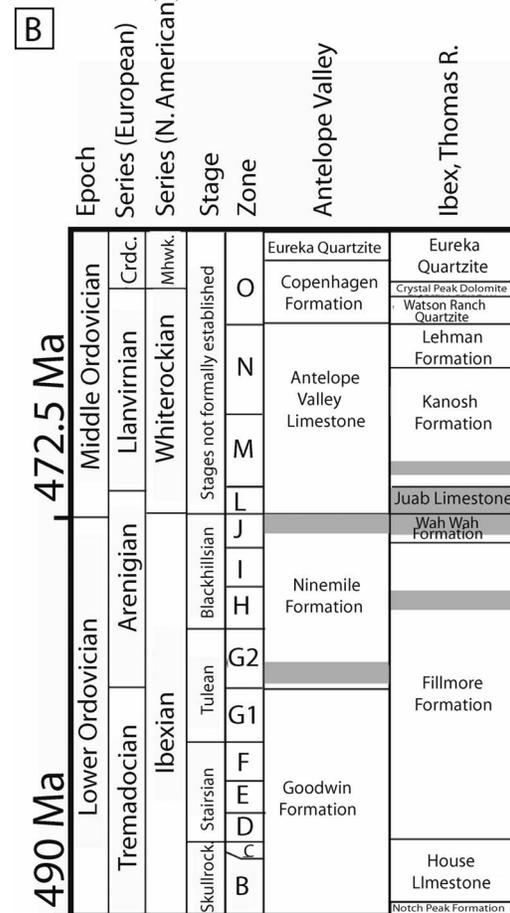


FIGURE 2—Location of samples and stratigraphy. A) Location of sections studied. B) Biostratigraphic and lithostratigraphic framework of Lower and Middle Ordovician rocks in the Basin and Range area. Gray bars = intervals sampled for this study.

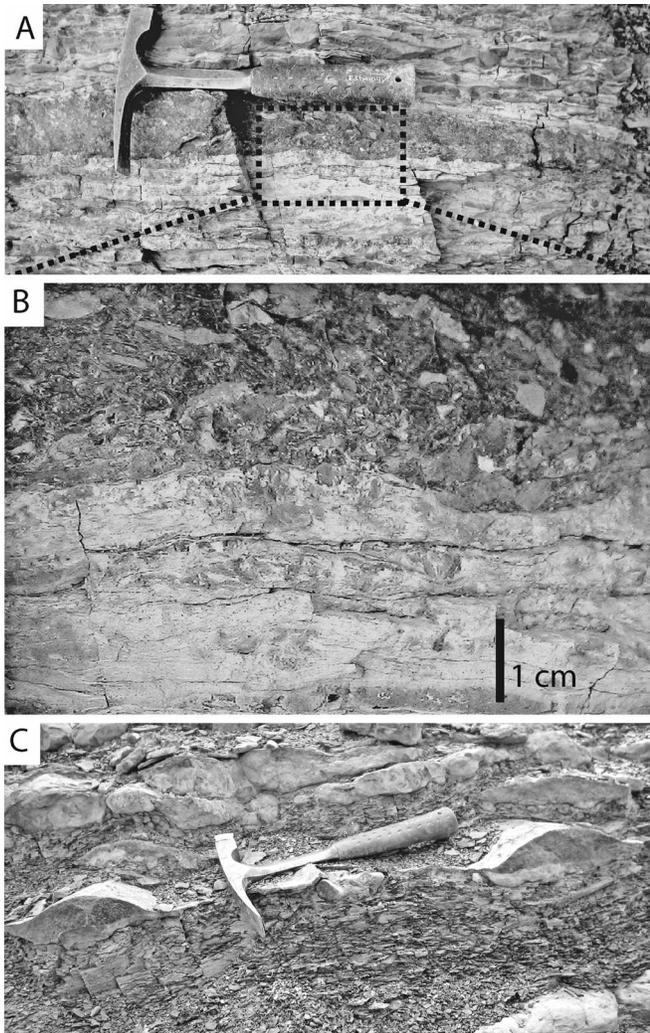


FIGURE 3—A) Tabular storm-generated grainstone event bed in shallow subtidal wackestone facies of the Wah Wah Formation, Thomas Range. B) Detail of A. Note imbricated intraclasts and erosional contact with underlying, unreworked sediments. C) Grainstone megaripple set probably generated by combined flow from deep subtidal shale-carbonate mudstone facies of the lower Kanosh Formation, Ibex. Hammer length = 28 cm.

and Aigner, 1991), the term storm bed is used here exclusively to denote coarse-grained, bioclast-supported beds with erosional bases. The term background beds is used to refer to a variety of fine-grained sediment types within which bioclastic storm beds occur, including shales, carbonate mudstones, and wackestones. These beds reflect a broad spectrum of sedimentation modes, ranging from slow, nearly continuous accumulation to episodic fallout of fine-grained sediments during the waning phases of storms that left no other record. The term background bed is intended to imply, not that these beds record continuous deposition, but simply that they are likely to be more stratigraphically complete, less stratigraphically disordered, less time averaged, and less physically reworked than bioclastic storm beds from the same units.

Samples were taken from within single biostratigraphic zones of stratigraphic units characterized by environmental stability and minimal faunal turnover (Fig. 2B). Each sample represents a single discrete bed at a single locality; no replicate samples are included in analyses. The data set includes 7 storm beds and 15 background beds from the Wah Wah Formation at Ibex and in the Thomas Range, Utah; 5 storm beds and 10 background beds from the Juab Limestone at Ibex (both Wah Wah and Juab Formations; Finnegan and Droser, 2005); 4 storm beds and 7 background beds from the lower Kanosh Formation at Ibex (Boyer and Droser,

2003); 2 storm beds and 9 background beds from the upper Fillmore Formation at Ibex (Hintze, 1973); 2 storm beds and 3 background beds from the lower Ninemile Formation in Ninemile Canyon, Antelope Range, Nevada (Ross, 1970); and 1 storm bed and 2 background beds from the upper Ninemile Formation at Whiterock Narrows (Ross et al., 1991; Fortey and Droser, 1996). Measured sections of these units are available in the references cited above; more detailed sections showing the positions of samples are available from the authors upon request.

Sampling protocols differed according to the lithology and fossil content of beds. Most storm beds and background beds with abundant skeletal material were collected as ~7 kg bulk samples, while those with more dispersed skeletal material were excavated in the field until a sufficient quantity of identifiable skeletal elements was recovered. Two storm beds from the Wah Wah Formation were censused with multiple quadrat counts on exposed bedding surfaces, using a 100 cm² quadrat. All other samples were broken apart in the laboratory using a hammer and chisel, following parting surfaces whenever possible.

Samples were examined with a binocular microscope, and all shell elements were identified to genus level when possible. Most could be identified to genus based on the published taxonomic literature (Ross, 1951, 1967, 1970; Hintze, 1953; Cooper, 1956; Jensen, 1967; Johns, 1994; Fortey and Droser, 1996, 1999; Adrain et al., 2001; Popov et al., 2002; Holmer et al., 2005). Individuals clearly distinct from others in the assemblage but not assignable to described genera were also counted. Several relatively rare brachiopod genera were clearly distinct but could not be identified owing to lack of well-preserved internals. Most mollusks and echinoderms could not be identified below the ordinal or family level because of poor preservation resulting from postmortem dissolution and disarticulation, respectively. Species-level identifications were not attempted in any case. Given the relative rarity of co-occurring congeneric species in the Lower Paleozoic (Westrop and Adrain, 1998), genera are assumed to be adequate proxies for species-level faunal patterns.

In keeping with paleoecological convention, only shell elements larger than 2 mm in longest dimension were counted. The only macroscopic taxa routinely excluded by this criterion are paleocopid ostracodes, which are extremely abundant in both background beds and storm beds of the lower Kanosh Formation, often forming the primary matrix of the latter. The following were counted as individuals: cranidia or pygidia of trilobites; brachiopod pedicle or brachial valves; leperditiid ostracode valves; steinkerns of aragonitic nautiloids, gastropods, and bivalves; and colonies or colony fragments of bryozoans, sponges, and calathid and receptaculitid algae. For echinoderms, only calyx plates and holdfasts were counted to minimize the ratio of skeletal elements to individuals. Though it is certain that the average skeletal-element-to-individual ratio varies significantly among these groups (Gilinsky and Bennington, 1994), this applies equally to storm beds and background beds and so should have no effect on comparisons between the two.

Effort was made to avoid counting parts and counterparts as separate individuals, but this doubtless happened in many collections. This should not alter relative abundance patterns, however, unless some taxa have a greater likelihood of being identifiable in both part and counterpart than others. In the relatively few instances in which shell elements were articulated or clearly associated, only one individual was counted. Because of their fragility and the consequent bias against preservation in storm-generated beds, phosphatic-shelled brachiopods and the thin sclerites of plumulitid machaeridians were excluded.

This study examines the two fundamental components of diversity (Hurlbert, 1971; Magurran, 1988; Hayek and Buzas, 1997; Buzas and Hayek, 2005): richness (the number of taxa present) and evenness (the equitability of taxon abundances). Rarefaction (Sanders, 1968; Hurlbert, 1971; Simberloff, 1972) was used to normalize richness to a standard sample size of 65 individuals ($E_{s_{65}}$), the size of the smallest sample. At this relatively small sample size, rarefied richness is highly influenced by the evenness of the sample (Olszewski, 2004; Peters, 2004a). For this reason, evenness was measured using Hurlbert's (1971) probability of

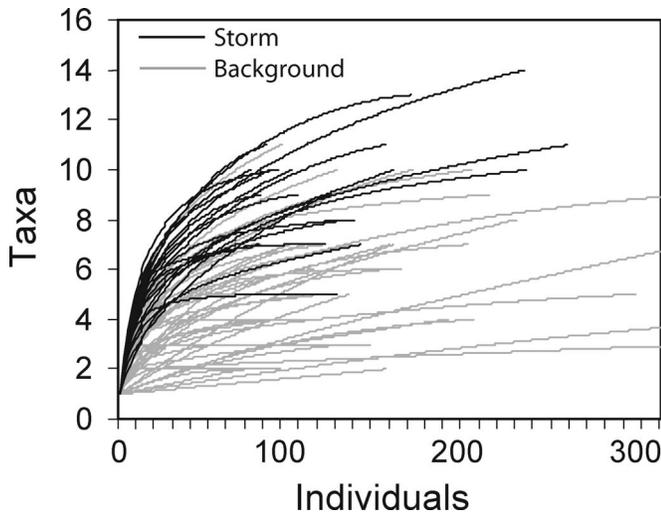


FIGURE 4—Rarefaction curves for all storm beds and background beds in the data set.

interspecific encounter, a metric ranging from 0 (minimal evenness) to 1 (maximum evenness), which can be explicitly related to rarefaction curves (Olszewski, 2004). Peters's E_{ss} , an alternative evenness index that performs better at very low richness values (Peters, 2004a) gives very similar results. Rarefaction analyses and nonparametric comparison tests were performed with the PAST software package (Hammer et al., 2001), which was also used for detrended correspondence analysis (DCA) of faunal composition in co-occurring storm beds and background beds. Because it does not assume the linear relationships between taxon abundances assumed by principal components analysis and because it corrects for the arch effect and gradient compression often observed in correspondence analysis (Hill and Gauch, 1980; Miller et al., 2001), DCA is particularly well suited for analyzing ecological data. Detrended correspondence analyses were performed separately for each stratigraphic unit, using the relative abundance matrix and default settings for axis rescaling (yes) and segment number (26). Although they were included in evenness and diversity analyses, for the DCA analyses all taxa that occurred in multiple samples but were not uniquely identifiable (i.e., Gastropod indet.) were excluded. This was done to avoid spurious correlations based on indeterminate identifications—two samples that both included Gastropod indet. in their faunal lists would be treated by DCA as if they had a taxon in common, even though the individuals may be of completely different genera. Taxa that were not identifiable to genus but occurred in only one sample or were consistently recognizable in multiple samples (e.g., High-spined gastropod genus A) were included.

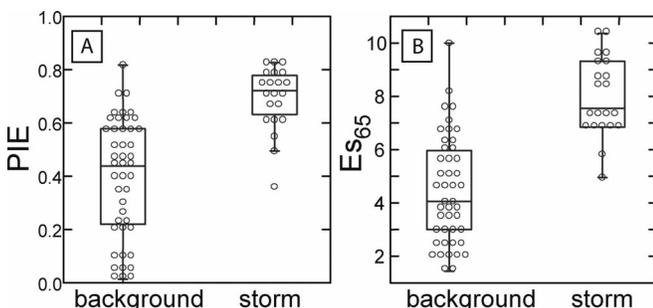


FIGURE 5—Distributions for background vs. storm beds. A) Evenness values (PIE). B) Rarefied richness values at E_{s65} . Horizontal bars = medians; boxes = second and third quartiles. PIE = probability of interspecific encounter. E_{s65} = standard sample size of 65 individuals.

TABLE 1—Comparisons of average rarefied richness (E_{s65}) and evenness (PIE) between background beds and storm beds for each of the six sampled units. PIE = probability of interspecific encounter. E_{s65} = standard sample size of 65 individuals.

Unit	Average PIE		Average E_{s65}	
	Background	Storm	Background	Storm
Wah Wah Formation	0.47	0.71	5.6	8.5
Juab Limestone	0.20	0.68	3.3	8.3
Fillmore Formation	0.61	0.69	6.2	7.2
Lower Ninemile Formation	0.08	0.59	3.4	7.1
Upper Ninemile Formation	0.41	0.80	5.0	6.8
Lower Kanosh Formation	0.46	0.72	2.7	7.9

RESULTS

Rarefaction curves for all 67 samples are plotted in Figure 4. While there is overlap between storm beds and background beds, storm beds have generally higher evenness (Fig. 5A) and rarefied richness (Fig. 5B) than background beds. Standard nonparametric comparison tests show that these differences are highly significant: Mann–Whitney U-test, $p < .0001$; Kolmogorov–Smirnov test, $p < .0001$ for both evenness and rarefied richness comparisons. Storm beds have an average evenness of 0.69, and their average richness at a sample size of 65 individuals (E_{s65}) is 8.0; background beds have an average evenness of 0.4, and an average E_{s65} of 4.5. The proportional difference in average richness is maintained at larger sample sizes, though fewer samples can be included; the average E_{s150} of storm beds is 10.8 ($n = 6$), while that of background beds is 6.0 ($n = 17$).

Because original diversity structure and taphonomic regime vary across the environments represented by individual stratigraphic units, a more meaningful comparison is between background beds and storm beds from the same stratigraphic units (Table 1). Interestingly, while the diversity structure (evenness and sampled richness) of background beds varies significantly among the six sampled stratigraphic units (Fig. 6A), there is very little variation in the diversity structure of storm beds, nearly all of which plot within the same small graphical region (Fig. 6B).

To examine this pattern in more detail, all possible pairwise contrasts between storm beds and co-occurring background beds ($n = 209$) are plotted in Figure 7. In 93.0% of such comparisons, storm beds have greater evenness than background beds (Fig. 7A); storm beds have greater rarefied richness (E_{s65}) than background beds in 96.5% of pairwise contrasts (Fig. 7B). This figure clearly shows a positive correlation between evenness and rarefied richness (Fig. 7C), the mathematical basis of which has been discussed by others (Hurlbert, 1971; Hayek and Buzas, 1997; Peters, 2004a; Olszewski, 2004). While fewer samples can be considered, the same basic pattern is observed when only trilobites (Fig. 8A) or rhyconelliform brachiopods (Fig. 8B) are considered, demonstrating that the diversity differences are not driven by a single group.

All samples in each unit were ordinated using DCA to investigate the faunal structure of the data sets (Fig. 9; taxon scores presented in Supplementary Data¹). The most notable pattern that emerges from these ordinations is that the distributions of storm bed and background bed DCA axis 1 scores are highly overlapping in the upper Fillmore, Wah Wah, and Juab Formations, whereas in the Ninemile and Kanosh Formations they do not overlap. The polarization of storm beds and background beds in the latter units is primarily attributable to the fact that, while most taxa in Fillmore, Wah Wah, and Juab storm beds are also found in background beds, many taxa in the Ninemile and Kanosh datasets occur exclusively in storm beds. The taphonomic significance of this pattern is considered in the second part of the discussion below.

¹ www.paleo.ku.edu/palaios.

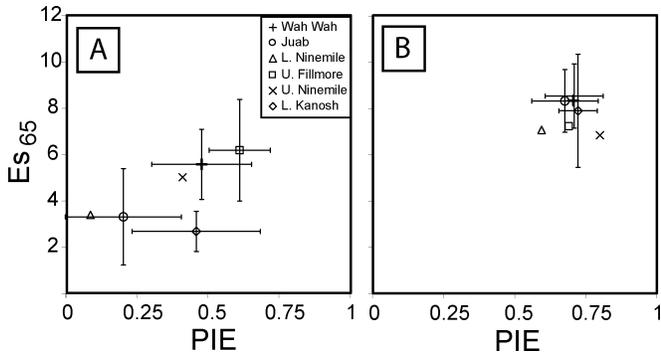


FIGURE 6—Crossplots of average rarefied richness (Es_{65}) and evenness (PIE) for (A) background beds and (B) storm beds from each of the six sampled formations. One standard-deviation-error bars are plotted for averages of three or more samples. Differences in average richness and evenness apparent in background beds cannot be recognized in storm beds. PIE = probability of interspecific encounter. Es_{65} = standard sample size of 65 individuals.

DISCUSSION

Potential Taphonomic Biases

Differences between background beds and storm beds could potentially be generated by differential shell destruction. Because reworked shell material is often highly fragmented, a much lower proportion of shell fragments are identifiable in storm beds than in background beds. This effect, however, is expected to deplete, rather than enrich, the sampled diversity of storm beds relative to background beds. Bioerosional and geochemical regimes can vary significantly among sediment types (Best and Kidwell, 2001; Best et al., 2001), and greater diversity in storm beds

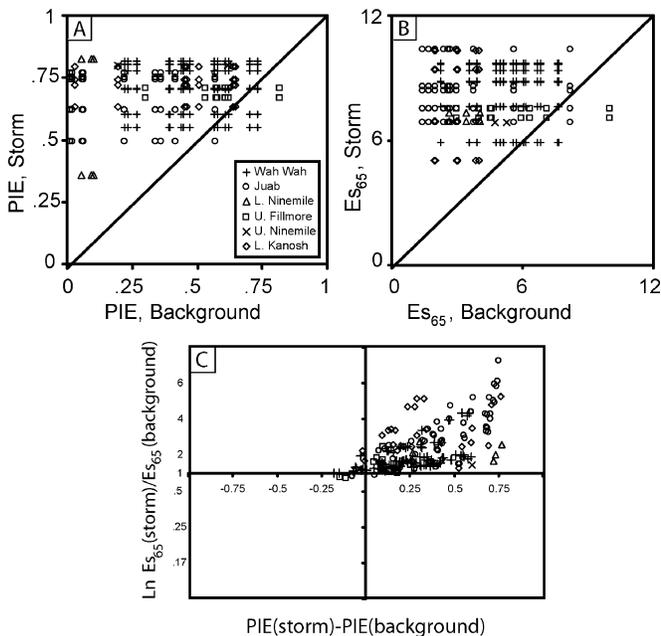


FIGURE 7—Pairwise comparisons of storm beds and background beds. Crossplots of all possible pairwise combinations of storm beds and background beds with respect to evenness (A) and rarefied richness at a sample size of 65 individuals (B). Evenness is measured using Hurlbert's (1971) PIE metric, and rarefied richness (Es_{65}) is calculated using Krebs's (1989) formulation of Sanders's (1968) rarefaction procedure. The close relationship between these two diversity metrics at small sample sizes is apparent when evenness and rarefied richness differences are crossplotted (C) for all possible combinations of storm beds and background beds. Rarefied richness values are compared using quotients, whereas, because PIE is nonlinear, evenness values are compared using arithmetic differences. PIE = probability of interspecific encounter. Es_{65} = standard sample size of 65 individuals.

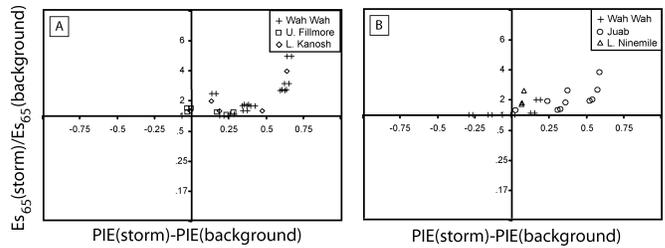


FIGURE 8—Differences in evenness (PIE) and rarefied richness (Es_{65}) for all possible pairwise comparisons of trilobite diversity (A) and brachiopod diversity (B) in storm-generated beds and co-occurring background beds. Relatively few comparisons are possible because only four storm beds from three units contained more than 65 trilobite individuals, while five storm beds from three units contained more than 65 brachiopod individuals. Axis labels are the same as in Figure 7A. PIE = probability of interspecific encounter. Es_{65} = standard sample size of 65 individuals.

would be expected if coarse carbonate substrates have lower rates of shell destruction than fine-grained sediments. While some work suggests that shell destruction rates should be higher in siliciclastics than in carbonates, this cannot explain consistent differences between grainstones and wackestones within carbonate-dominated units. Moreover, studies of recent molluscan death assemblages suggest that rates of shell destruction are in fact higher in carbonate-dominated sediments than in fine-grained siliciclastic sediments, possibly due to more favorable bottom conditions for bioeroders (Kidwell et al., 2005).

Another potential explanation for the difference is differential preservation of originally aragonitic taxa. For instance, Bush and Bambach (2004) noted that, in siliciclastic sequences of Late Ordovician and Silurian age, mudstones frequently preserve the casts and molds of dissolved aragonitic bivalves but that these casts and molds rarely survive storm reworking and hence bivalves are often depleted in storm beds. Enhanced preservation of aragonitic taxa in background beds would again

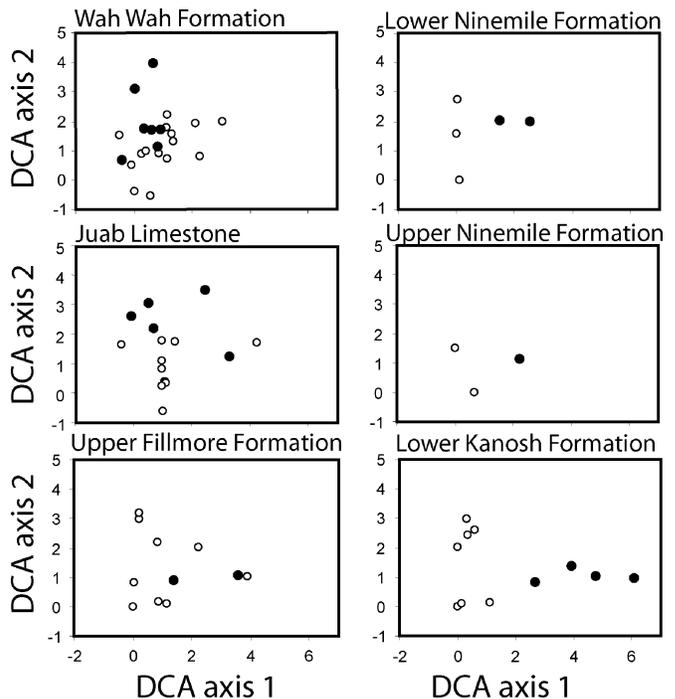


FIGURE 9—Scatterplots of DCA axes 1 and 2 for each of the six studied units. Percentages of total variance accounted for by axes 1 and 2 for each formation: Wah Wah: axis 1, 63%; axis 2, 30%. Juab: axis 1, 74%; axis 2, 22%. Fillmore: axis 1, 89%; axis 2, 8%. Lower Ninemile: axis 1, 98%; axis 2, 2%. Upper Ninemile: axis 1, 98%; axis 2, 2%. Kanosh: axis 1, 74%; axis 2, 23%. DCA = detrended correspondence analysis.

tend to diminish the sampled diversity of storm beds relative to background beds, so this effect cannot account for the difference. In our data set, there is little difference between storm and background beds in the proportion of aragonitic individuals, which are represented exclusively by casts and molds in both bed types. Originally aragonitic individuals account for, on average, 6.2% of individuals in storm beds and 4.4% of individuals in background beds, and this difference is not statistically significant (Mann–Whitney U-test, $p = 0.12$; Kolmogorov–Smirnov test, $p = 0.11$).

Storm beds in our data set are generally strongly lithified with few internal parting surfaces, while less disturbed background beds often preserve numerous bedding surfaces. Thus, most shell elements in storm beds are exposed along fracture surfaces rather than bedding surfaces. This may impose a bias in favor of shell elements, such as those of asaphid trilobites or strophomenoid brachiopods, which are large and smooth and thus more likely to form fracture surfaces. Given the general negative correlation between body size and abundance, underrepresentation of small taxa will tend to increase evenness. While this effect may contribute to the observed differences, it does not fully explain them. Sampling only the upper and lower surfaces of storm beds, where this bias should not apply, does not significantly change evenness estimates. In fact two of the most diverse storm bed samples from the Wah Wah Formation (BP 3.75 and BP 7.75) include only individuals exposed on the upper surface of beds.

Sources of Increased Diversity: Spatiotemporal Averaging versus Taphonomic Feedback

The relationship between background beds and storm beds has parallels to that between living communities and their death assemblages, and some analogous processes are involved. Studies of recent mollusk and mollusk-brachiopod death assemblages (Kidwell, 2002; Olszewski and Kidwell, 2002; Kowalewski et al., 2003) have found that both the richness and the evenness of the death assemblage is generally elevated relative to that of co-occurring living communities. Kidwell (2002) and Olszewski and Kidwell (2002) found that this could not be explained by passive time averaging of static local communities, and they postulated that it might result from averaging of ecologically volatile local communities. Alternatively, they note that it could result from allochthonous inputs of shells from other habitats or preferential destruction of the smallest, often very abundant, species. All of these processes may also contribute to the observed differences between storm beds and background beds. A further potential source of added diversity in storm beds was discussed by Kidwell and Jablonski (1983) and Kidwell (1986b), who highlighted the importance of taphonomic feedback in facilitating seafloor colonization by taxa that require firm or hard substrates. Storm reworking concentrates shells and intraclasts into discrete layers that armor the seafloor and reduce turbidity; in the Ordovician these layers were particularly subject to early cementation (Palmer and Wilson, 2004), thus providing attachment surfaces for encrusters.

Both transport of material from other habitats and shell bed colonization would have the effect of adding taxa to storm beds that are not present, or are very rarely sampled, in background beds. In contrast, a quite different mechanism for increasing diversity in reworked beds is suggested by the observation that within a given habitat all species distributions are to a greater or lesser extent patchy, and these patches can be volatile on ecological time scales (Miller, 1988; Bennington, 2003). Thus, background sedimentation censuses a complex and constantly shifting patch mosaic. Significant within-habitat sediment reworking and redeposition is likely to result in both spatial and temporal homogenization of this patch mosaic, increasing the average faunal completeness of storm beds relative to background beds and thereby increasing their richness. If the fossil assemblages preserved in background beds have generally high dominance (low evenness) but significant volatility in rank-order abundance, spatiotemporal averaging will also tend to increase evenness

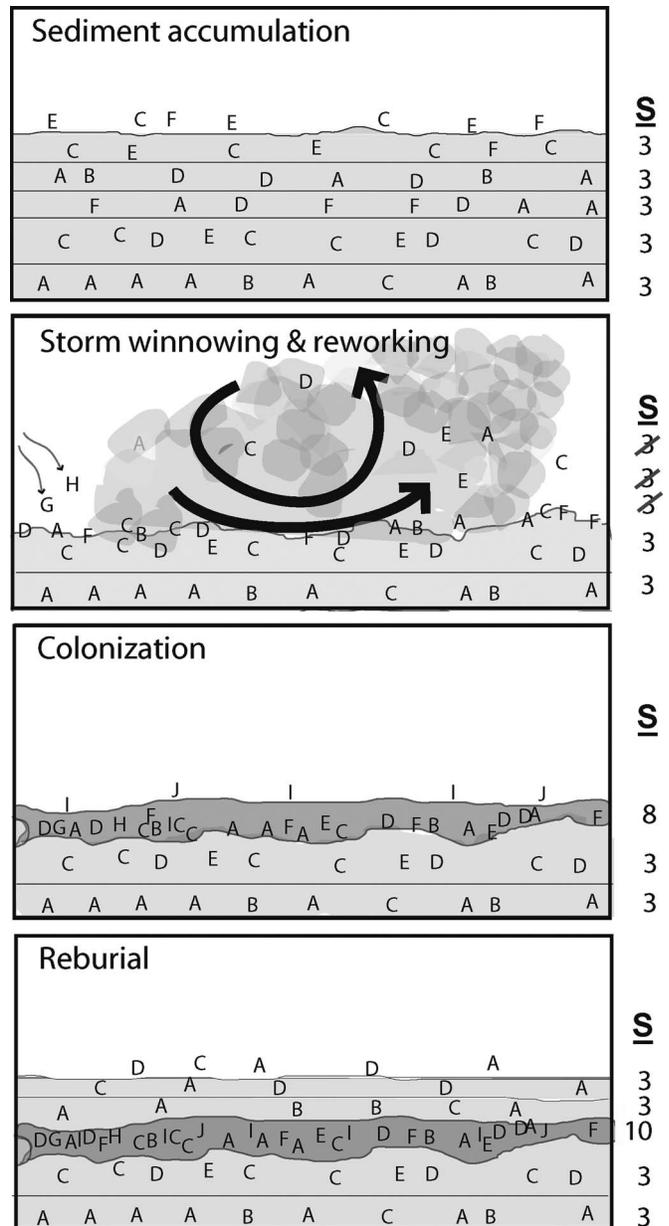


FIGURE 10—A cartoon illustrating the formation history of a hypothetical storm bed. Initially, several beds recording background sedimentation preserve patchy species distributions. While there are six species present in the habitat (A–F), no more than three are present at any one place and time. Waves and currents associated with a storm winnow away fine sediments in the upper three beds and may introduce rare out-of-habitat remains (G, H). Following this winnowing, the remaining bioclastic concentration may be lithified and colonized by taxa (I, J) that are excluded from soft-bottomed habitats. The resulting bed thus has substantially higher diversity than the background beds from which it was originally derived. The right-hand column indicates the number of species (S) present in each habitat or bed.

by averaging together the most abundant taxa from different patches. Figure 10 illustrates the cumulative effect of all of these processes—spatiotemporal averaging, out-of-habitat transport, and taphonomic feedback—on the sampled diversity of a hypothetical storm bed. Because it has been shown to be relatively rare in most depositional environments (Miller, 1988; Miller et al., 1992; Flessa, 1998; Behrensmeier et al., 2000), out-of-habitat transport is depicted here as a minor contributor.

The relative importance of these processes in generating the observed differences in sampled diversity between storm beds and background beds can be evaluated with the DCA ordinations. If the greater richness and

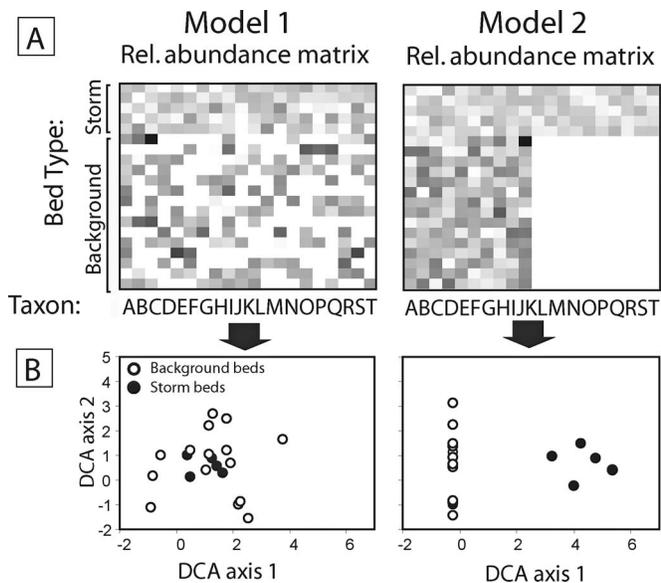


FIGURE 11—Ordination of model data sets illustrating two end-member cases for increased diversity of storm beds relative to background beds. A) Relative abundance matrices illustrating spatiotemporal averaging (left) and taphonomic feedback scenarios (see text for further explanation). Grayscale boxes correspond to relative abundance: black, >33%; white = absent. B) Scatterplots of DCA axes 1 and 2 for the model matrixes illustrated in A. Using model 1, storm beds plot entirely within the ordination space defined by the background beds, while they are polarized along DCA axis 1 in model 2. DCA = detrended correspondence analysis.

evenness of storm beds is caused primarily by taphonomic feedback (or, less plausibly, out-of-habitat transport), DCA is expected to polarize storm-bed samples and background-bed samples along DCA axis 1 owing to the presence of a suite of taxa in storm beds that are absent or very rare in background beds. If, however, increased richness and evenness in storm beds is caused primarily by *in situ* averaging of background beds with varying faunal compositions and relative abundance structures, the extremes of DCA axis 1 should be occupied by background beds having few taxa in common, with homogenized storm beds tending to fall in the middle of this range. In the pure end-member case in which increased diversity is entirely due to such averaging, a similar distribution of storm beds and background beds is expected along DCA axis 2—that is, the ordination space occupied by storm beds should be completely contained within that occupied by background beds.

Figure 11 illustrates model relative abundance matrices representing these two end-member cases (Fig. 11A) and scatterplots of DCA axis 1 and 2 scores for ordinations of the modeled samples (Fig. 11B). These models are intended only to illustrate the behavior of DCA given two extreme scenarios and are not intended as formal simulations exploring the full range of possibilities. In model 1, 20 taxa (columns A–T) are present in the 15 background bed samples (rows), but because they are patchily distributed, the average richness of a single bed recording background sedimentation is only 10. Five storm beds were produced in each case by generating three background beds and averaging their relative abundance matrices. As expected, the storm beds plot within the ordination space defined by the background beds. In model 2, only 10 taxa (columns A–J) are present in the background beds, but each taxon occurs in every bed. In this model the storm beds were produced, not by averaging, but by including an additional 10 taxa (columns K–T), which do not occur in background beds, to simulate the effects of taphonomic feedback. The addition of these taxa polarizes storm beds and background beds along DCA axis 1, overwhelming the relative abundance variation among background beds, which is instead expressed primarily along DCA axis 2. Reducing the proportion of taxa that occur exclusively in storm beds increases the scatter of background beds along DCA axis 1, but, in

all cases we examined, storm beds and background beds are completely separated along this axis.

The ordinations of these end-member models provide a useful framework for examining the results of DCA on the six sampled units (Fig. 9). It should be noted, however, that this approach assumes that the sampled background beds contain the full range of within-habitat faunal variation. Obviously, when the number of sampled background beds is low, as is the case in both Ninemile data sets, this assumption is likely to be invalid, and caution should be used in drawing conclusions from any comparative analysis.

In the shallow subtidal and carbonate-dominated upper Fillmore, Wah Wah, and Juab Formations, storm bed samples fall within the range of DCA axis 1 values exhibited by background bed samples, suggesting that spatiotemporal averaging is dominantly responsible for their elevated diversity. In contrast to the pure averaging model, however, the distributions of storm beds and background beds in the Wah Wah and Juab are partially separated along DCA axis 2. Although evaluating percent variance explained is not a straightforward procedure in DCA, the relatively high eigenvalues associated with DCA axis 2 in the Wah Wah and Juab suggest that in these units taphonomic feedback plays a significant but secondary role in increasing the diversity of storm beds.

There is complete separation of storm beds and background beds along DCA axis 1 in the deeper-water, fine clastic-dominated environments represented by the Kanosh and Ninemile Formations. Although the Ninemile results should be interpreted cautiously given the small number of samples, field inspection of storm-bed float blocks that could not be traced to individual beds in outcrop confirms that they typically contain numerous taxa not commonly encountered in the shale beds that constitute the bulk of the formation. In the case of the Kanosh, sampling is adequate to demonstrate that taphonomic feedback is the dominant source of increased diversity in storm beds. Notably, most (but not all) of the taxa that score highly on DCA axis 1 in the Kanosh are obligate encrusters such as pedunculate brachiopods, bryozoans, and crinoid echinoderms (see the Supplementary Data¹). A second factor that may be significant is the fact that the sampled background beds are primarily dark shales that have been interpreted to represent oxygen-stressed conditions (McDowell, 1987; Boyer and Droser, 2003). This accounts for their strikingly low diversity (see the Supplementary Data¹) and suggests that, in addition to lack of suitable substrates, many of the taxa occurring in storm beds were excluded by dysaerobic conditions during intervals of background deposition.

Taken as a whole, these data imply that spatiotemporal averaging of patchily distributed taxa is primarily responsible for the high diversity of shell beds in shallow, carbonate-dominated settings, while taphonomic feedback is the more important process in deeper, fine-clastic-dominated settings. Substrates thus appear to be a major limiting factor—hardgrounds, firm grounds, and sponge-algal buildups—are evident during intervals of background deposition in each of the shallow carbonate units and likely provided nearby habitat patches for encrusters and associated fauna. In contrast, bioclastic storm beds would have provided the only such habitat in the deeper, shale-dominated units.

There is also an evolutionary signal that should be considered. Most of the units examined here are of Early Ordovician age and, thus, largely precede the dramatic pulse of global diversification that took place between the Early and Late Ordovician (Miller and Foote, 1996). Many of the groups that experienced major radiations during this interval, including rhynchonelliform brachiopods, bryozoans, echinoderms, sponges, and corals, are dominantly encrusters. Indeed, the diversification of echinoderms has been explicitly related to substrate availability (Guensberg and Sprinkle, 1992). Thus, the relative insignificance of taphonomic feedback in the Lower Ordovician units may be in part attributable to a paucity of encrusters compared to Middle Ordovician and younger assemblages.

Implications for Measuring Alpha Diversity

While storm beds contain, on average, a greater proportion of resident taxa than background beds, they do not necessarily record a faithful signal

of paleocommunity structure either within or between depositional environments (Fig. 6). There are therefore important trade-offs to be considered in choosing samples for analyses of diversity patterns across environments and through time. For example, the trilobite alpha diversity data set analyzed by Westrop and Adrain (1998) and Adrain et al. (2000) contains many samples derived from storm beds. These results imply that those samples are likely to contain a high proportion of resident taxa and are therefore appropriate for such an analysis. These results also suggest, however, that the same data set may not be appropriate for an analysis of diversity structure, so that Adrain and Westrop's (2005) finding of invariant trilobite community evenness across depositional environments and throughout the Lower Paleozoic should be viewed with caution. The high proportion of storm beds in their data set could help to explain discrepancies between their findings and those of Peters (2004a, 2004b), who preferentially sampled unreworked beds (S. Peters, personal communication, 2002).

Most of the Paleozoic community samples examined by Powell and Kowalewski (2002) and Bush and Bambach (2004) are derived from storm beds, but most of their Cenozoic samples are not. These results raise the possibility that true differences in diversity structure between Paleozoic and Cenozoic communities may be even more marked than they are in their analyses. It is also possible, however, that even unreworked Cenozoic sediments represent considerably more temporal averaging than Paleozoic storm beds (see below).

Temporal Trends in the Resolution of the Marine Fossil Record

All of the units considered here predate the Late Ordovician increase in bioturbation intensity documented in Basin and Range strata by Droser and Bottjer (1989). This increase, and subsequent increases in the depth and extent of bioturbation (Thayer, 1979, 1983; Larson and Rhoads, 1983) may have diminished the average temporal resolution of the marine soft-substrate fossil record (Sepkoski, 1982; Brandt, 1986; Sepkoski et al., 1991; Kowalewski and Bambach, 2003). If this is the case, the observed pattern of differences between storm beds and background beds may be limited to the Lower Paleozoic. After this time, strong differences should not necessarily be expected because background sediments may already be thoroughly homogenized by bioturbation prior to storm reworking. Few appropriate data are available from younger rocks to test this prediction, but it is interesting to note that in their paleocommunity analysis of the Main Glauconite Bed of the Eocene Crockett Formation in Texas, Zuschin and Stanton (2002) found little difference in diversity structure between storm and background beds. Similarly, Miller et al. (1992) found that in Salt River Bay, St. Croix, reworking by Hurricane Hugo had relatively minor effects on the diversity structure of the molluscan death assemblage. New data from other units throughout the Paleozoic are necessary to determine whether this represents a general trend in the temporal and ecological resolution of the fossil record.

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