Evolution of Fossil Invertebrate Communities: Additional Factors

A model of change in Paleozoic invertebrate communities was proposed by Bretsky (*1*) from which relative community diversity and stability gradients presumably can be deduced. However, analysis of Bretsky's model makes evident several possible sources of confusion. Bretsky implies that depth of water is interchangeable with "onshore" and "offshore" environments. This generalization seems to rely on the assumption that, with respect to texture of terrigenous clastics, coarse-grained sediment indicates onshore and fine-grained sediment indicates offshore conditions. Deductions of habitat from this assumption can be in error, since grain size of terrigenous clastic material is primarily a function of the competency of the water to hold sediment in suspension or as traction load; therefore grain size may not be related to either depth of water or distance from shore.

The question of bathymetry and the size of grains in sediments is further complicated by the particular conditions of Paleozoic seas and their predominantly carbonate deposits (*2*). The preponderance of carbonate rocks in the Paleozoic suggests that restriction of the study to areas of "terrigenous clastic environments" (*1*) may mean oversimplification. For example, in areas where information on submarine profiles across the Paleozoic continental shelves is sufficiently detailed (*2, 3*), several general characteristics are encountered: (i) continental shelves were generally wider than at present, and (ii) they commonly included areas of reef development along the outer edges of the platforms in a manner similar to development of coral islands along the present Great Bahama Bank (*4*). If this is generally true of the Paleozoic, the terms onshore and offshore must be clearly defined and cautiously applied, since offshore fossil assemblages could have originated in the intertidal zone (or at least in very shallow water), even though geographically separated from the continental shoreline by several hundred kilometers. This condition could significantly affect conclusions based on comparisons of community diversity between onshore and offshore environments during the Paleozoic.

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Taylor and Sheehan object to my use of the terms onshore and offshore; the point is indeed well taken. Predominantly carbonate reef, bank, and shoal deposits clearly were important on and along the outer fringes of Paleozoic shelves, and their occurrence obviously tended to alter a regular offshore deepening.

The main thesis of my report was, however, to outline seemingly consistent or changing patterns in the structure of some Paleozoic marine communities, and to determine whether or not "the structure of a particular community of organisms in a given habitat has ever changed with time" (*1*). Be it oversimplication or merely simplification, evolutionary patterns at the community level were most apparent in terrigenous clastic environments, and it was within this context—and not without a certain degree of trepidation—that I chose to organize these Paleozoic marine data on a bathymetric scale. The rationale was that, regardless of the complexity introduced into the terrigenous clastic sedimentary pattern [Shaw's (*2*) allochthonous sedimentary pattern], there tends to be an overall seaward decrease in grade size.

The details of the pattern reflect not only mechanical energy within the sea, but also the grade of the debris brought in from the land. This point was emphasized in my statement that "some 'offshore' populations (those usually common in muds and silty muds) may occasionally have dominated 'onshore' environments in which fine sediment textures, lowered rates of deposition, and generally narrow fluctuations in the physical-chemical regime prevailed" (*3*).

Examples of Paleozoic autochthonous sedimentary environments (*2*) certainly complicate the pattern of evolution of Paleozoic communities by introducing a whole host of taxa rarely abundant in allochthonous environments. Even more importantly, salinity, substratum, and current energy—not simply bathymetry—are considered to be the most important ecological factors determining the position of the Bahamian and Floridian faunal communities (*4*), with which Paleozoic carbonate-depositional regimes are most frequently analogized. Still most workers refer to nearshore and offshore (tidal and subtidal) autochthonous environmental settings. [An especially good example is Laporte's study of the New York Devonian Manlius Formation (*5*).] Within this onshore-to-offshore environmental picture, the organisms comprising benthic marine communities, in carbonate environments, could then be viewed throughout the Paleozoic as having occupied definite positions relative to the shore, lagoon, bank, or reef; changes in their number and kinds could be related to a definite autochthonous sedimentary pattern, which again appears to show a general onshore-to-offshore sequence (*2*).

The analogies of Paleozoic carbonate regimes to those of the Recent Bahamian type have permitted greater understanding of the horizontal (paleogeographic) or biofacies relations, but there must be continued interest in the vertical (community evolution) relations. Patterns of community evolution, in predominantly carbonate or autochthonous environments, may then be compared and combined with the general allochthonous or continental-margin scheme. In either case, there can be little disagreement with Taylor and Sheehan's contention that continued use of the terms onshore and offshore must be qualified and must be "clearly defined and cautiously applied."

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