Evolution of Paleozoic Marine Invertebrate Communities

Abstract. *Communities of Paleozoic shelf invertebrates underwent varied rates of change in faunal composition. Notable changes took place during Late Devonian–Early Mississippian time and were most noticeable in offshore brachiopod-dominated communities. Near-shore molluscan communities remained relatively stable throughout the Paleozoic.*

Recent recognition of many ancient marine communities of invertebrates (Fig. 1) has increased the likelihood of mapping of parallel benthic communities (*1*) for any segment of the geologic past. [The fossil communities in almost every instance are recognized from Petersen's (*2*) statistical definition of communities as consistently recurrent associations of species.] This growing body of knowledge not only permits more detailed explanations of the evolutionary development of selected taxonomic groups, but also raises the issue of community stability and evolution over extended periods of geologic time. Previous workers (*3*, *4*) have discussed stability and structure in Recent communities; many have suggested that increased faunal diversity and food-web complexity should lead to the selection of more-stable and presumably longer-lasting communities; but Hedgpeth (*5*) comments that some communities of low diversity and simple structure may be very stable. Many problems of the evolution of stable community structure —what kinds of communities are stable, where they are most stable, and how long they remain stable—remain virtually untouched (*6*). My report deals only with the evolution of Paleozoic marine communities of invertebrates occupying terrigenous clastic environments; I do not consider carbonate environments.

The structure of marine benthic communities is generally thought to be relatively uncomplicated (*7*); the basic pattern was established during the Early Paleozoic (*3*). In fact Late Ordovician marine invertebrate assemblages contain recognizable nearshore faunas of a distinctly modern aspect (*8*). The prospects for study of community evolution during the Paleozoic, however, are especially promising, because this was the time of initial phylogenetic radiation of the major invertebrate groups. Thus it seems probable that adaptive shifts, radiations, and extinctions may have been directly related to changing community structures. Testing of the hypothesis of increased faunal diversity as a clue to fossil-community stability awaits further quantified data and may not be applicable because paleoecologists work only with apparent and not with real diversity gradients. The length of time a community maintains a constant faunal composition would seem to provide a key to the evolution of stable community structure. By tracing the evolution of marine-invertebrate community structures throughout a long period of geologic time, we can begin to document variable rates of change in the faunal composition of communities, and thus recognize particular benthonic environmental settings in which community stability or instability exists.

My studies of fossil communities in the Upper Ordovician strata of eastern North America (*8*) led to a survey of contributions to the study of Paleozoic fossil assemblages. This survey emphasized that, when the entire Paleozoic is considered, the total faunal composition of offshore benthonic communities changed more rapidly than that of nearshore communities. The offshore communities underwent a period of particularly rapid faunal change during Late Devonian–Early Mississippian time.

Five major Paleozoic shelf associations (Table 1) can be recognized on the basis of faunal continuity or of maintenance of community stability over long periods. Each association is composed of numerous stratigraphically defined communities (Fig. 1). The naming of these communities either follows that of the individual investigator (see Fig. 1; references are given in parentheses) or has been chosen by me to express the most conspicuous and presumably dominant faunal elements in the fossil assemblage. Also I found it convenient to organize the data on a generalized bathymetric scale, realizing that bathymetry is only one of many possible physical, chemical, or biotic variables that may influence the geographic distribution of these fossil associations, but that it does express the usual coarse (onshore) to fine (offshore) sediment pattern (*20*). In fact substratum type may have been the most important factor in the overall distribution and faunal composition of Paleozoic shelf communities, just as it is today (*1*).

The most consistently recurrent association of faunas, the linguloid-molluscan association, is found in the environments nearest to shore, where environmental fluctuations were undoubtedly more frequent than in deeper waters. This nearshore faunal association remained stable from the Late Ordovician to the Late Permian. It was consistently dominated by large numbers of 'infaunal" (*1*) detritus-feeding nuculoid bivalves and suspension-feeding linguloid brachiopods; and "epifaunal" (*1*) bellerophontid gastropods, which, by analogy with the morphologically similar Recent pleurotomariids, probably were herbivorous (macrophagous). Rhynchonellid brachiopods (*Orthorhynchula, Camarotoechia*) was common in the linguloid-molluscan association throughout the Early Paleozoic, as well as some genera of mussel-like bivalves (ambonychiids and modiomorphids). Sometime during the Early Mississippian these forms were replaced, or their vacated niches were filled, by other epifaunal, attached organisms: spiriferid brachiopods (*Crurithyris*), and pectinoid and myalinid bivalve molluscs.

The deeper sublittoral environments, presumably in a physically less rigorous regime, had large numbers and great diversity of brachiopods. The brachiopod assemblages of the Early Paleozoic shelves usually comprised two distinct communities: The strophomenid-trilobite association, which appears most commonly in silts and muddy silts, is composed of a variety of strophomenid

Table 1. Outline of Paleozoic fossil associations. The five associations are diagramed in Fig. 1 and depicted as occupying relative onshore and offshore environments.

Association	General environmental setting	Duration
Linguloid-molluscan	Sand, silt; onshore	Ordovician–Permian
Strophomenid-trilobite	Silt, mud; offshore	Ordovician–Devonian
Atrypid-bryozoan	Mud; onshore, offshore	Ordovician–Devonian
Productid-chonetid	Silty mud, mud; onshore?, offshore	Devonian–Permian
Fusulinid-palaeotextulariid	Lime mud; offshore	Pennsylvanian–Permian

and orthid (Enteletacea) brachiopods, trilobites, and crinoids. The less abundant protobranch bivalve molluscs and pleurotomariid gastropods, both of which were probably detritus-feeders, occurred in localized patches. The atrypid-bryozoan association is more common in muds, and apparently occupied an outer sublittoral position on the Early Paleozoic shelves. I point out, however, that one may infer from detailed study of Late Ordovician communities (*8*) 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. The abundant faunal elements of the atrypid-bryozoan association were atrypid and pentamerid brachiopods and trepostomatous bryozoans, with locally abundant murchisoniid gastropods, pterioid bivalves, and orthid (Orthacea) brachiopods. Although a certain amount of faunal mixing occurred between these two Early Paleozoic brachiopod associations, they formed quite distinct faunal associations until the Late Devonian.

Brachiopod-dominated shelf faunas of the Mississippian and later Paleozoic exhibited no such well-defined separation, and thus are grouped as the productid-chonetid association. The Late Paleozoic outer-shelf environments contained a variety of productid and chonetid brachiopods associated with athyroid brachiopods, crinoids, bryozoans, and some large (supposedly infaunal) bivalve molluscs (Praecardioida). Domination of the outer shelf by brachiopods was challenged only during the Late Paleozoic by the appearance of a very diverse benthic assemblage of arenaceous Foraminifera (palaeotextulariids), which also included large numbers of fusulinids, crinoids, and bryozoans and some echinoderms. This fusulinid-palaeotextulariid association is a well-documented assemblage, and is thought by Stevens (*18*) to have been outer sublittoral. Faunal mixing also took place here between the productid-chonetid association and fusulinid-palaeotextulariid association; but again, as in the Early Paleozoic, a characteristic recurrence of dominant species emphasized a distinct separation.

This brief resumé of Paleozoic community evolution points out a major faunal change of many benthic shelf faunas near the end of the Devonian Period. The predominantly nearshore linguloid-molluscan association underwent noticeable change in the taxonomic composition of the epifaunal articulate brachiopods and byssate bivalve molluscs, but the linguloid brachiopods, bellerophontid gastropods, and nuculoid bivalves remained constant up to the Late Permian. The brachiopod-dominated outer-shelf faunas, however, experienced a period of major faunal replacement. The strophomenid-trilobite and atrypid-bryozoan associations ended abruptly as distinctly separable units sometime during the Late Devonian or Early Missisippian and were replaced by another brachiopod association, the productid-chonetid association, which was joined somewhat later by the fusulinid-paleotextulariid association.

The major reorganization of the outer-shelf faunas relative to the inner ones raises interesting questions concerning the stability of benthic community structure and the factors controlling the consistency of these com-

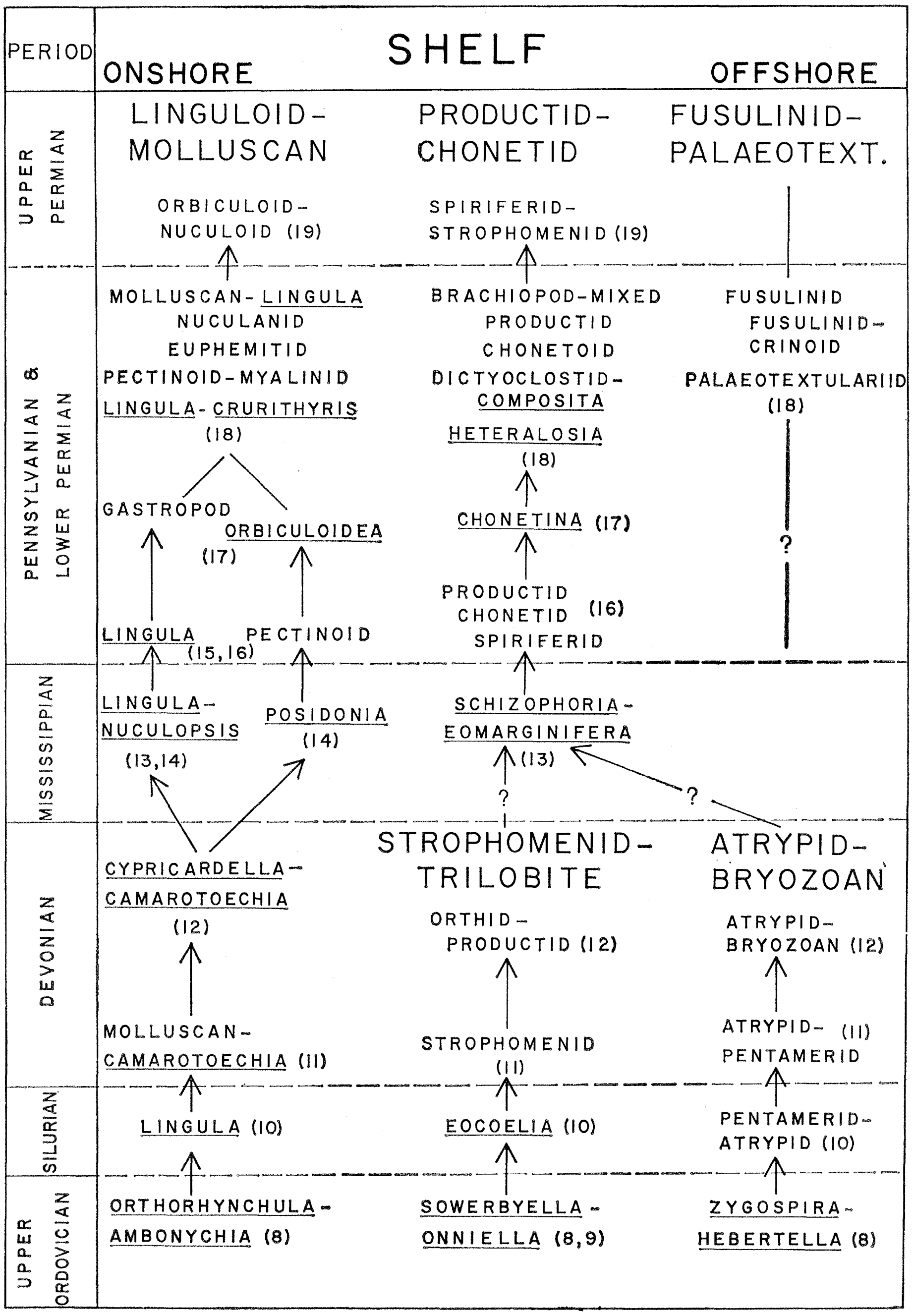

Fig. 1. Evolution of Paleozoic marine-invertebrate community structure. The onshore-to-offshore axis is a generalized interpretation of the probable relative environmental setting; it does not negate the possibility of occasional nearshore, quiet-water fusulinid, atrypid, or pentamerid faunas. References appear in parentheses.

munities through a prolonged period of geologic time. Diversity, expressed as the number of variable niches, should be limited by the monotony of environmental conditions in offshore waters, but also by the wider fluctuations of physical parameters in nearshore environments. There is marked increase in generic diversity from nearshore to offshore communities, but an accompanying decrease in community stability. Presumably an Early Paleozoic selection for species efficiency established the linguloid, bellerophontid, and nuculoid fauna in the rigorous nearshore physical regime, and favorable selection continued throughout the Paleozoic to perpetuate a stable nearshore community structure, with the replacement of only some taxa. Simple or uncomplicated community structure (abundant individuals but few species) does not necessarily mean that the community is at an early stage of evolution (*5*), but may show that it is quite stable and possibly very old. The linguloid-molluscan association at the end of the Paleozoic demonstrates an old but stable community structure. I suggest that further evolutionary studies of benthic marine communities of invertebrates will show more-rapid faunal changes (that is, less community stability) in the physically monotonous outer sublittoral communities.

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Pesticides: Transatlantic Movements in the Northeast Trades

Abstract. *Concentrations of chlorinated hydrocarbons in airborne dust carried by the trade winds from the European-African land areas to Barbados range from less than 1 to 164 parts per billion. The lower limit of the average content of 1 cubic meter of air is* 7.8×10^{-14} *gram. The contributions of river-borne and atmospherically transported pesticides to parts of the marine environment are calculated approximately and compared. The amounts of pesticides contributed to the tropical Atlantic by the trade winds appear to be comparable to those carried to the sea by major river systems.*

The transport and distribution of pesticides through the world ecosystem have been attributed to a combination of atmospheric and hydrospheric (oceanic and fluvial) currents (*1*), yet their relative contributions remain unclear. The high concentrations of residues of pesticides found in shearwaters *Puffinus tenuirostris* and *P. griseus* from the Pacific Ocean and skuas *Catharacta skua* from Antarctica suggest that coastal areas are not the sites of ingestion (*1*).

Various lines of evidence indicate air transport: (i) the codistillation of chlorinated hydrocarbons with water (*2*), and (ii) their detection in air and rainwater (*3*) and in atmospheric dust originating in Texas and subsequently deposited in Ohio (*4*). These observations, however, are not sufficient to support the hypothesis that much of the pesticides present in marine organisms was atmospherically transported to the oceans from the continents.

Complementing such work is the observation that the mineral talc that is used as a carrier and diluent for pesticides occurs in the solid-mineral phases of rains, glaciers, and rivers and in dusts recovered from the atmosphere in concentrations much higher than expected from natural occurrences (*5*); its existence in airborne particulate matter over the sea (*6*) suggests a link with the global dispersion of pesticides.

Although talc is perhaps diagnostic of the presence of insecticides, its use as a quantitative tracer is not fully warranted; it is gradually being displaced in pesticides by water or light petroleum bases. Furthermore, some insecticides are dispersed in Fuller's earth, a mixture of minerals not readily analyzed by x-ray diffraction.

Large-scale tropospheric transport from continents to oceans can best be approached by investigation of the three main zones of movement of air masses: the equatorial easterlies, the temperate westerlies, and the polar easterlies. Gram quantities of airborne particulate matter carried by the equatorial easterlies, the trade winds, over 6000 km from Europe and Africa across the Atlantic to Barbados were collected (*7*). Pronounced seasonal variations in the magnetic and biological fractions correlated with wind patterns off the African coast. Mineralogical and biological observations pointed to a continental origin of the solids, with Europe and Africa as the most likely sources. Each sample comprised a large fraction of the particulate material in several million cubic meters of air. An input rate of solid phases to the tropical Atlantic sediments of 0.6×10^{-4} cm/year was suggested (*6*). Knowledge of the pesticide levels in such materials would permit similar calculations of their inputs, for which purpose the Barbados samples have been analyzed.

The collecting screens (*6*), facing the wind, were made of 0.5-mm-diameter monofilament nylon woven to give about 50 percent voids; they were coated with a 50-percent water solution of glycerin for our work; collection efficiency was about 50 percent for particles larger than 1 μ. Rigorous standards of cleanliness minimized contamination by local dusts, which has always proved to be trivial. For blank runs for the pesticide analyses, acetone-washed dust was applied to screens, with subsequent treatment as for the real samples. Less than 100 pg of any of the DDT compounds (*8*) or other pesticides per gram of sample was found.

The dust samples were Soxhlet-extracted for 6 hours with a 2:1 mixture of hexane and acetone. Blank runs, using the same solvent volumes, extraction times, and glassware, were made before and several times during the course of the analyses; less than 250