# Species-abundance Models: An Ecological Approach to Inferring Paleoenvironment and Resolving Paleoecological Change in the Waldron Shale (Silurian)

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*The Silurian Waldron Shale preserves a diverse marine fossil assemblage dominated by epibenthic suspension feeders. Three paleocommunities, distinguished from one another by taxonomic composition, relative abundance of taxa, and fossil distribution, are represented in the Waldron.*

*The Biohermal Community exists above storm-wave base and has the greatest taxonomic richness and evenness. Species-abundance data for non-strophomenid brachiopods most closely fit a log-normal distribution. The Inter-reef Community occurs below storm-wave base, contains fewer species, and is less even in abundance distribution. Rank-abundance data for the non-strophomenid brachiopod fauna most closely fit a log-series distribution. The Deeper Platform Community exists below storm-wave base, and may have experienced lower oxygen concentrations. The community has low species richness and abundance, and is dominated by strophomenid brachiopods. This community cannot be fitted to either the log-series or log-normal distributions, but resembles a broken stick distribution.*

*In all three Waldron communities, water depth, habitat heterogeneity, biotic interactions, and disturbance may have played important roles in determining biodiversity. General environmental conditions predicted by species-abundance models are congruent with paleoenvironmental conclusions drawn from sedimentological and paleontological data, suggesting that some paleoenvironmental and paleoecological conditions can be inferred from the ecology of a fossil indicator taxon. Many of the factors controlling diversity in biological communities may have remained the same over much of Phanerozoic time, possibly making analysis of the link between the Recent and the Paleozoic a viable foundation for predictive models for some aspects of community dynamics.*

## INTRODUCTION

Modern ecologists often focus on species diversity when trying to describe and compare communities (e.g., Fischer, 1960; Huston, 1979; Rex et al., 1993; Gee and Warwick, 1996). Species richness, or the number of species present in a community, and species abundance, or the number of individuals of each species, together comprise diversity. There are a number of reasons why diversity is commonly selected as a useful community characteristic, but perhaps most important is the relationship of species diversity to environmental factors such as productivity (e.g., Abrams, 1995; Fraser and Currie, 1996), habitat heterogeneity (e.g., O'Connor, 1991; Death and Winterbourn, 1995), disturbance (e.g., Dayton and Hessler, 1972; Sousa, 1979, 1984; Kukert and Smith, 1992; Wootton, 1994), and species interactions (e.g., Connell, 1961; Tevesz and McCall, 1983; Wilson, 1990). Models that account for the distribution of individuals among species observed in many modern communities generally are thought to be the most complete mathematical description of species-abundance data (e.g., May 1975, 1981; Magurran, 1988). Indices of diversity that incorporate species richness and evenness, such as the Shannon-Weiner index, are useful means of comparing communities but do not carry as much information about ecological and environmental conditions as the theoretically-based abundance models.

There are four main models of species-abundance distribution: (1) the geometric series; (2) the log-series; (3) the log-normal distribution; and (4) the broken stick distribution (Magurran, 1988). The models are thought to reflect differences in the degree of habitat heterogeneity, time without disturbance, resource availability, and niche preemption occurring in a community.

The geometric series appears as a straight line with a steep negative slope when plotted on a log-abundance vs. species-rank graph. Field data from a wide range of modern communities have shown that the geometric series typically occurs in harsh environments or in communities that are in very early stages of succession (Whittaker, 1965). The log-series distribution is very closely related to the geometric series (May, 1975), and many authors make little or no distinction between the two distributions. Like the geometric series, the log-series distribution predicts a larger proportion of rare species and a rather small number of abundant species. It most frequently occurs in situations where one or a few factors dominate the ecology of a community (Magurran, 1988). For example, Magurran (1981) demonstrated that understory plants in a conifer forest, where light is the single most important factor controlling diversity, fit a log-series distribution, and Miller (1986) showed that some Pleistocene fossil assemblages also approached log-series and geometric distributions in estuarine environments, where salinity and substrate were chiefly responsible for controlling diversity.

The log-normal distribution is exhibited by the majority of modern communities studied, and is generally thought to be indicative of those that are large, mature, and varied (May, 1981; Magurran, 1988). In a log-normal distribu-

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tion, there are relatively few rare species, few abundant species, and a larger proportion of species of intermediate abundance. Although the significance of this distribution in large data sets is disputed, communities conforming to a log-normal distribution differ fundamentally from communities with log-series or geometric distributions. Specifically, resources often are more abundant and partitioned more equitably in a community with log-normal distribution, variation in habitat is greater, and sources of environmental stress are fewer.

The broken stick model has been described as the "biologically realistic expression of a uniform distribution," and occurs in communities where an ecological factor is being shared rather equally among species (Magurran, 1988). The broken stick distribution is rare in nature, but has been shown to occur in some situations (e.g., King, 1964).

Although species-abundance models cannot successfully be applied to every community, and their ecological significance is still debated, the models often are associated with communities in particular ecological settings. Ecologists most commonly use species-abundance models to monitor the response of diversity when known environmental changes are affected. For example, Patrick (1973) showed that a natural diatom community had a log-normal distribution before the environment was stressed with organic pollutants, whereupon diversity declined and the community fit a log-series or geometric distribution. Species-abundance models also are becoming increasingly appreciated in conservation situations, where they may serve as discriminatory tools in assessing the quality or character of environments. Recently, Hayek and Buzas (1997) have advocated "SHE" analysis, which may facilitate the recognition of species distributions in sample data, particularly in cases where there is statistical convergence between the various distributions. For most applications, SHE analysis will be the best way to distinguish between community data sets.

In this paper, the biological characteristics of three depositional facies described by Feldman (1989) are examined, and a synecological investigation of the Upper Wenlockian Waldron Shale macrobiota of southeastern Indiana is presented. The Biohermal, Inter-reef, and Deeper Platform communities can be distinguished by taxonomic make-up, structure, environmental parameters, and "demographics" in the sense of population density and distribution. Ecological conclusions then are drawn from the paleontological data, using ecological theory, to illustrate the mutual relevance of modern ecology and the Waldron fossil assemblage.

## GEOLOGIC SETTING OF STUDY AREA

The Waldron Shale (Silurian: Wenlockian) is a mixed carbonate-clastic unit, up to five meters in thickness, deposited on a shallow cratonic platform between the Michigan and Illinois basins (Droste and Shaver, 1985; Shaver and Sunderman, 1989). Locally, the Waldron has wave-cut, disconformable contacts with both the underlying Laurel Member of the Salamonie Dolomite and the overlying Louisville Limestone (Halleck, 1973; Conkin et al., 1992). This investigation was conducted in southeastern Indiana, and included five locations from the north-south trending Waldron outcrop belt in Bartholomew, Jennings, and Shelby Counties, Indiana (Fig. 1).

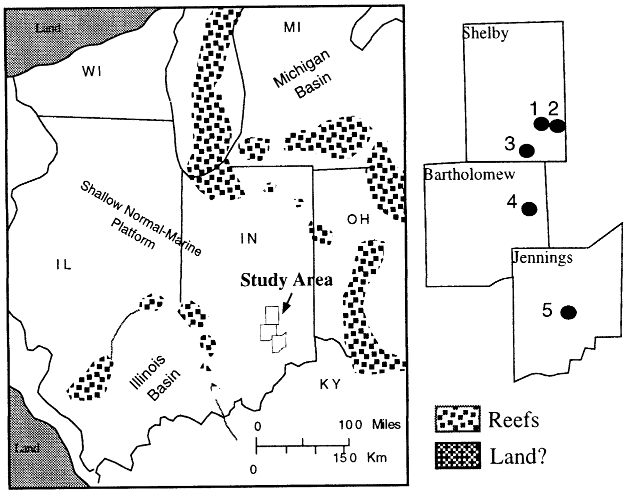

**FIGURE 1**—Paleogeographic reconstruction (adapted from Shaver, 1996) of the Midwestern U.S.A. and location of study area. Numbered dots are Waldron Shale exposures used in this study.

During the late Wenlockian, southeastern Indiana was positioned approximately 25 degrees south of the equator, and the area experienced a tropical to sub-tropical climate (Witzke, 1990). Reef and carbonate-bank facies fringed the study area to the north, west, and east, and partially restricted water circulation on the platform during low sea-level stands (Griest and Shaver, 1981; Shaver, 1996). Shaver (1996) identified four depositional cycles in the Silurian rocks of the Great Lakes region. Each cycle was characterized environmentally in terms of siliciclasticity, salinity, relative sea level, and biotic constituency (Shaver, 1996), and was within the estimated 1-million-year time frame of third-order sequences (Shaver, 1996; Ross and Ross, 1996). The Waldron represents the deeper water stage of one of these third-order cycles.

The diverse Waldron biota, dominated by sessile epifaunal suspension feeders, was first described by Hall (1864). Watkins (1996) reported echinoderms as the dominant skeletal elements in point-counted polished slabs. Similar Wenlockian assemblages have been described by Watkins and Hurst (1977), Jaanusson et al. (1979), Watkins (1979), and Taylor and Brett (1996).

Feldman (1989) has discussed the paleoenvironmental parameters associated with three facies he identified in the Waldron Shale of the study area. The facies relate to depth relative to storm-wave base, substrate firmness, and dissolved oxygen content in the sea water (Fig. 2), and correspond with specific paleocommunities that are described herein. Facies A is present near the base of the Waldron section, and is characterized by discontinuous skeletal tempestites and meter-scale algal-constructed microbioherms (Archer and Feldman, 1986). Storm currents affected this facies, and shale clasts are present in shell-bed tempestites concentrated around microbioherms (Feldman, 1989). Fossil distribution in this facies is patchy, with most skeletal elements concentrated around microbioherms. Facies A has an abrupt transition to Facies B at most locations, with the base of facies B marking the disappearance of microbioherms. Facies B is less fos-

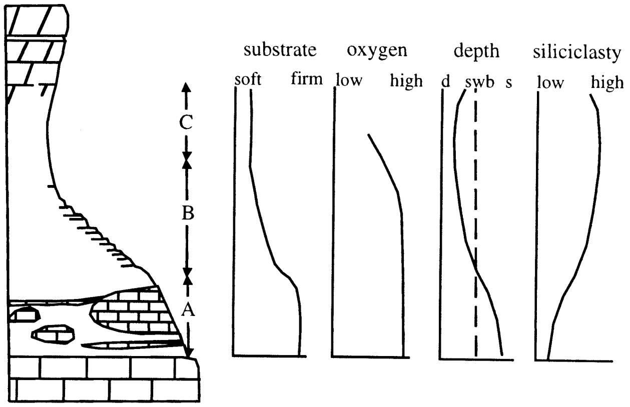

**FIGURE 2**—Generalized Waldron Section showing evolution of depositional environment; d = deep; s = shallow; swb = storm wave base (adapted from Feldman, 1989; Shaver, 1996).

siliferous than A and is dominated by 1-to-3-cm-thick, laterally continuous mudstone beds that alternate with less resistant shale beds. Fossils are distributed rather uniformly, but are typically more common near *Eucalyptocrinites crassus* holdfasts. We infer that storm currents occasionally affected the bottom in this environment, but intact multi-element skeletons commonly are preserved at the base of some mudstone beds that are thought to represent distal tempestites (Feldman, 1989). The contact between Facies B and C is gradational vertically over approximately 20 cm at most locations. Facies C occurs near the top of the Waldron section throughout much of the study area and is distinguished by a very low abundance of macrofossils. Feldman (1989) attributed the paucity of fossils in this facies to stressful conditions such as low oxygen concentration. Deposition probably occurred below storm-wave base (Feldman, 1989). Each of the paleoenvironments represented by these three facies closely corresponds with one paleocommunity.

Feldman (1989) also discussed the taphonomic and diagenetic processes at work in the Waldron Shale. He found little evidence for dissolution of skeletal elements, extensive bioturbation, or long-distance transport of skeletal elements. He concluded that "a large proportion and perhaps all of the original shelled inhabitants of these facies were preserved" (Feldman, 1989, p.154). Such conditions make the Waldron well suited for paleoecological investigations.

## MATERIALS AND METHODS

A community is defined herein as an association of taxa recognizable through time and space by their recurrence in similar relative abundance (i.e., recurrent community concept of Raup and Stanley, 1978). Because gradients in physical and chemical conditions exist in the natural world, it is acknowledged that in many instances the biological communities supported by those conditions must also be part of a continuum. The spatial and temporal scale to which this community concept can be applied is also flexible. For the present investigation, paleocommunities occupying several tens to hundreds of square kilometers of sea floor and spanning less than 1 million years were examined.

Stratigraphic sections were measured at each location (Appendix), and the boundaries between facies were distinguished based on the criteria outlined by Feldman (1989). Examples of such criteria include bedforms, lithology, presence/absence of microbioherms, and vertical position within the Waldron section. Species-abundance data were collected from randomly sampled slabs. Because data collection was constrained by the nature of the outcrop, no predetermined sampling regime was employed. Rather, bedding-plane samples were collected from as many places and horizons as feasible from each of the three facies at several localities. Each slab was scrubbed, and all fossils (exposed anywhere on the sample) that were visible with the unaided eye were identified. Skeletal elements that could not be identified in the field because of poor exposure or weathering were not counted. To minimize inflation of the apparent abundance of organisms with multi-element skeletons, only critical or defining portions of their morphology were counted as individuals. For example, crinoids were counted only when their calyx or holdfast was present, and only cephalons of trilobites were included in the data set. Trepostome bryozoans were not counted, but their presence was noted. Sample size was considered adequate when the addition of new taxa diminished to less than approximately one new taxon per 100 counts. Because the data collected for this investigation were voluminous and field based, only representative samples were deposited in the paleontological collection at Denison University.

Many fine specimens revealing important biological interactions, such as secondary tiering (sensu Ausich and Bottjer, 1982) on living crinoids, were recovered (Peters and Bork, 1998). In cross-section exposures, such as quarry walls, the lateral position of skeletal elements was recorded. Lateral variability in fossil concentration in the Waldron is an important characteristic that has been noted by many workers (Hall, 1864, 1881; Foerste, 1898; Halleck, 1973; Feldman, 1987, 1989).

Abundance data were calculated as percent of fauna. Diversity, *H'*, in each paleocommunity was measured using the proportional abundance Shannon-Weiner index (Magurran, 1988). This index is more sensitive to species richness than other indices of diversity (e.g., the Simpson's index) and also is influenced by abundance distribution, giving the index good discriminating ability (Magurran, 1988). Evenness, *E,* in each paleocommunity was calculated as the ratio of observed diversity to maximum diversity (where maximum diversity occurs when all species are equally abundant), or $E = H'/\ln S$, where S is the total number of species (Magurran, 1988).

Rank-abundance plots incorporating the entire fauna were generated for each community. When plotted on a y-log, x-normal coordinate plane, species-abundance data conforming to a particular model present a characteristic curve shape. To evaluate Waldron species-abundance distribution in terms of these models, we inspected rank-abundance plots and tested the mathematical fit of the Waldron data to the two models most closely resembling the observed curve shape. In the present examples, the data were compared to the log-series and log-normal distributions using chi-squared goodness of fit tests, the null hypothesis being that the data were drawn from a population having the tested distribution. The log-series distribution takes the form $\propto x$, $\propto x^2/2 \ldots \propto x^n/n$, where $\propto x$ is the number of species predicted to have one individual, $\propto x^2/2$ is the number of species predicted to have two individuals, and so on (Magurran, 1988). The value of x is determined by iterating the term $S/N=[(1-x)/x][-\ln(1-x)]$, S being the total number of species and N being the total number of individuals sampled. The term $\propto = N(1-x)/x$ is an index of diversity and is used to determine the expected number of species in each abundance class.

Because a small sample size can give an inadequate representation of the rare species in a community, the truncated log-normal distribution, which corrects for the unsampled rare species in one tail of the normal curve, was tested with Waldron species-abundance data. Magurran (1988) described the calculations used to determine the expected number of species in each abundance class and also the caveats of interpreting log-normal distributions.

In addition to rank-abundance plots for the entire biota of each community, plots for the non-strophomenid brachiopod fauna also were examined. Species-abundance models are based ecologically, and taxa selected for model application must have similar ecologies. It is conceivable that different taxa present in the same biological community could fit different models. Most non-strophomenid brachiopods from the Waldron presumably had a functional pedicle. They were chosen as ecological "indicator species" because they are interpreted to have been sensitive to such physical conditions as turbidity, substrate firmness, and oxygen concentration (Rudwick, 1970), and because they are abundant, readily preserved organisms with similar ecologies. Strophomenid brachiopods were omitted because they tend to be more tolerant of soft substrates and do not typically require attachment surfaces (Rudwick, 1970).

Indicator species commonly are used by modern ecologists when assessing the status of a community (Noss, 1989; Pearson, 1994), and all conclusions must be considered in terms of the ecology of the indicator taxon. Many modern applications focus on one or two species with ecologies that make them vulnerable to specific environmental contaminants. However, focusing on a taxon at a higher categorical level can reveal larger-scale environmental characteristics that influence community dynamics as a whole (Pearson and Cassola, 1992). This approach is particularly useful when there is uncertainty in whole-community data, or when counting individuals of some taxa poses problems.

## RESULTS

Waldron lithofacies defined by Feldman (1989) preserve paleocommunities distinguished from one another by (1) taxonomic composition, (2) rank-abundance of taxa, and (3) lateral distribution of organisms on the sea floor. Measured stratigraphic sections and approximate boundaries between paleocommunities are presented in Figure 3. Because of the essentially continuous deepening of the Waldron sea (Feldman, 1989; Shaver, 1996), paleocommunities are preserved in the succession shown in Figure 3 and do not recur at a single location. However, because of variable water depth in local depositional basins, particular communities could exist at different times at separate locations.

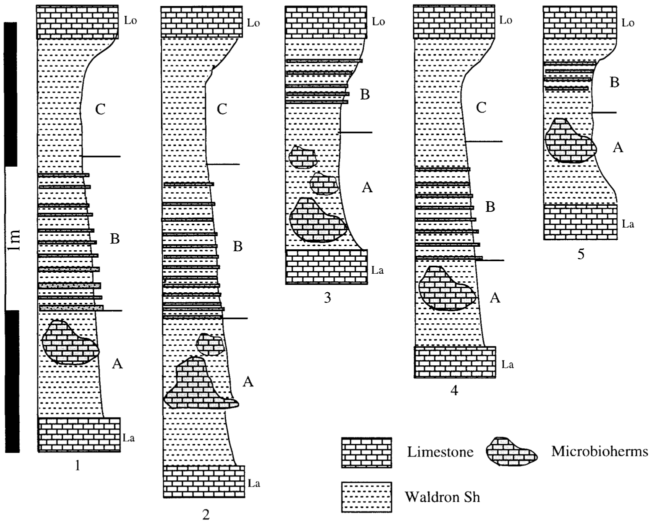

**FIGURE 3**—Sections showing thickness of Waldron Shale and approximate boundaries between paleocommunities; A = Facies A—Biohermal Community; B = Facies B—Inter-reef Community, C = Facies C—Deeper Platform Community; Lo = Louisville Limestone; La = Laurel Dolomite. Numbers correspond to locations in Figure 1 and in Appendix.

Table 1 and Figure 4 provide a summary of the species-abundance data associated with the Biohermal, Inter-reef, and Deeper Platform paleocommunities, and Figure 5 shows rank-abundance plots for whole-community data. Variation in paleocommunity composition and structure between localities is limited mostly to changes in rank position among some taxa of intermediate abundance. An exception to this is the lack of a complete Biohermal assemblage at location 5.

Whole-community species-abundance data were not mathematically fit to a model because of uncertainty in whole-community data resulting from the difficulty of counting individuals of such taxa as trilobites and bryozoans, and because variable eco-strategies employed by Waldron taxa make application of ecologically-based models problematic. However, species-abundance data for each community do differ, and there is a shift from log-normal-like distribution in the Biohermal Community to a geometric-like distribution in the Deeper Platform Community.

The Biohermal Community is associated with Feldman's (1989) facies A. It is the most diverse Waldron community and has the highest degree of evenness in its species-abundance distribution (Table 2; Fig. 5). Fossils are primarily concentrated near microbioherms and many species are preserved attached to these structures in living position.

Non-strophomenid brachiopod-abundance data for the Biohermal Community, graphically overlaid from three sampling locations, reveals consistency in rank-abundance plot (Fig. 6A). The rank-abundance plot is consistent with a log-normal distribution. Results of a chi-squared goodness-of-fit test do not allow rejection of the null hypothesis (data drawn from a log-normal distribution; Table 2). There were very few unsampled species in the community (calculated $<1$), as indicated by a very small area under the curve beyond the veil line (for full

**TABLE 1**—Species-abundance data for Waldron paleocommunities. N is the number of individuals counted, %NSBF is the percent of non-strophomenid brachiopod fauna, A is abundant, and C is common.

| Taxon | N= | % fauna | % NSBF | Taxon | N= | % fauna |
|---|---|---|---|---|---|---|
| Facies A: Biohermal Community | | | | | | |
| Non-Strophomenid Brachiopods | | | | Echinoderms | | |
| *Stegerhynchus indianense* | 642 | 35.6 | 43.8 | *Eucalyptocrinites crassus* | 37 | 2.1 |
| *Homoeospira evax* | 209 | 11.6 | 14.3 | *E. tuberculatus* | 15 | 0.8 |
| *Whitfieldella nitida* | 157 | 8.7 | 10.7 | *Lyriocrinus melissa* | 4 | 0.2 |
| *Atrypa reticularis* | 107 | 5.9 | 7.3 | *Stephanocrinus* sp. | 1 | 0.1 |
| *Howellella crispa* | 95 | 5.3 | 6.5 | *Lecanocrinus pusillus* | 1 | 0.1 |
| *Resserella waldronensis* | 63 | 3.5 | 4.3 | | | |
| *Anastrophia internascens* | 61 | 3.4 | 4.2 | Trilobites | | |
| *Mendacella circulus* | 36 | 2.0 | 2.5 | *Harpidella christi* | 32 | 1.8 |
| *Meristina maria* | 25 | 1.4 | 1.7 | *Calymene breviceps* | 21 | 1.2 |
| *Dictyonella reticulata* | 24 | 1.3 | 1.6 | *Glyptambon verrucosus* | 11 | 0.6 |
| *Rhynchotreta americana* | 19 | 1.1 | 1.3 | | | |
| *Sulcatina sulcata* | 16 | 0.9 | 1.1 | Miscellaneous | | |
| *Eospirifer radiatus* | 10 | 0.6 | 0.7 | *Favosites forbesi* | 58 | 3.2 |
| | | | | Platyceratid gastropods | 34 | 1.9 |
| Strophomenid Brachiopods | | | | *Fistulipora* sp. | 13 | 0.7 |
| *Fardenia subplana* | 54 | 3.0 | — | *Duncanella borealis* | 11 | 0.6 |
| *Strophodonta* sp. | 36 | 2.0 | — | *Astylospongia praemorsa* | 3 | 0.2 |
| *Leptaena rhomboidalis* | 8 | 0.4 | — | Ramose bryozoans | A | — |
| | | | | Fenestrate bryozoans | C | — |
| Facies B: Inter-reef Community | | | | | | |
| Non-Strophomenid Brachiopods | | | | Echinoderms | | |
| *Stegerhynchus indianense* | 1041 | 54.3 | 84.2 | *Eucalyptocrinites crassus* | 68 | 3.6 |
| *Homoeospira evax* | 71 | 3.7 | 5.7 | *Periechocrinus* sp. | 2 | 0.1 |
| *Resserella waldronensis* | 40 | 2.1 | 3.2 | *Glyptaster* sp. | 1 | 0.1 |
| *Howellella crispa* | 38 | 2.0 | 3.1 | | | |
| *Mendacella circulus* | 17 | 0.8 | 1.3 | Trilobites | | |
| *Rhynchotreta americana* | 13 | 0.7 | 1.0 | *Maurotarion christi* | 171 | 8.9 |
| *Atrypa reticularis* | 8 | 0.4 | 0.6 | *Calymene breviceps* | 66 | 3.4 |
| *Whitfieldella nitida* | 4 | 0.2 | 0.3 | *Glyptambon verrucosus* | 10 | 0.5 |
| *Dictyonella reticulata* | 2 | 0.1 | 0.2 | *Lichas* sp. | 9 | 0.5 |
| *Eospirifer radiatus* | 2 | 0.1 | 0.2 | | | |
| *Dicoloesia bilobata* | 1 | 0.1 | 0.1 | Miscellaneous | | |
| *Anastrophia internascens* | 1 | 0.1 | 0.1 | Platyceratid gastropods | 147 | 7.7 |
| | | | | *Fistulipora* sp. | 34 | 1.8 |
| Strophomenid Brachiopods | | | | *Favosites forbesi* | 14 | 0.7 |
| *Strophodonta* sp. | 103 | 5.4 | — | *Pterinea* sp. | 4 | 2.2 |
| *Fardenia subplana* | 24 | 1.2 | — | Ramose bryozoans | C | — |
| *Strophochonetes novascotica* | 23 | 1.2 | — | Fenestrate bryozoans | C | — |
| *Leptaena rhomboidalis* | 3 | 0.2 | — | | | |
| Facies C: Deeper Platform Community | | | | | | |
| Strophomenid Brachiopods | | | | Non-Strophomenid Brachiopods | | |
| *Strophodonta* sp. | 166 | 44.1 | | *Stegerhynchus indianese* | 42 | 11.1 |
| *Strophochonetes novascotica* | 154 | 41.0 | | *Resserella waldronensis* | 3 | 0.8 |
| *Fardenia subplana* | 9 | 2.4 | | *Atrypa reticularis* | 1 | 0.3 |
| | | | | Miscellaneous | | |
| | | | | *Fistulipora* sp. | 1 | 0.3 |

discussion see Magurran, 1988). Sample size was adequate and included most taxa of intermediate abundance (Fig. 7), and a number of rare taxa of less importance to species-abundance models.

The Inter-reef Community belongs to Feldman's (1989) facies B. This community has considerable taxonomic overlap with the Biohermal Community but is significantly less even in species-abundance distribution (Table 2). Many taxa common to both communities occur in different relative abundance (although *Stegerhynchus* is the numerically dominant fossil in both the Biohermal and Inter-reef communities). Trilobites, gastropods, and strophomenid brachiopods make up a larger proportion of the fauna in the Inter-reef Community. The number of individuals representing several guilds in each paleocommunity are shown graphically in Figure 4. In this example, guilds are defined as taxonomic groups having similar life strategies.

The rank-abundance plot for the non-strophomenid brachiopod fauna of the Inter-reef Community closely resembles a log-series distribution (Fig. 6B). Data from three collecting localities, graphically overlaid, show consistency in species-abundance distribution (Fig. 6B). Results of a chi-squared goodness-of-fit test indicate that the null hypoth-

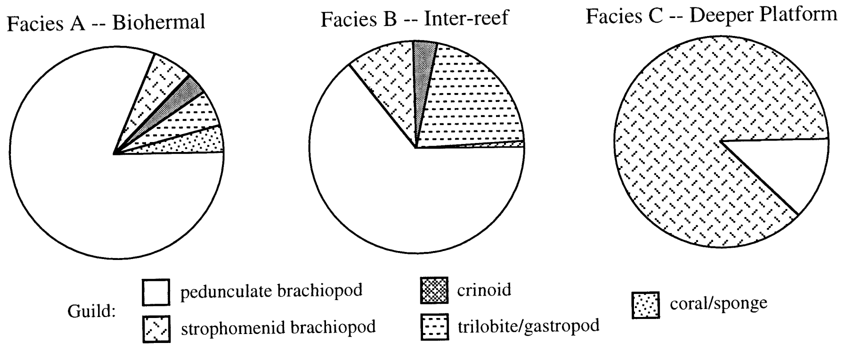

**FIGURE 4**—Guild structure of Waldron paleocommunities. Proportions based on number of individuals in each category.

esis (sample drawn from a population with log-series distribution) cannot be rejected (Table 2).

The Deeper Platform Community corresponds with Feldman's facies C and is a low-diversity, low-abundance community dominated by strophomenid brachiopods (Tables 1, 2; Fig. 4). This community does not occur at all locations and is restricted to deeper-water microbasins within the larger depositional basin. Species-abundance data for non-strophomenid brachiopods do not conform to either the log-series or log-normal distributions (Table 2). Species abundance for the strophomenid brachiopod fauna in this community resembles the broken stick distribution. However, because so few species are present, the data cannot be tested rigorously.

## DISCUSSION

Biodiversity in Waldron paleocommunities seems to be controlled primarily by habitat heterogeneity. In the lower Waldron, abundant firm substrates provided by microbioherms (Archer and Feldman, 1986), skeletal tempestites (Feldman, 1989), and *Eucalyptocrinites crassus* holdfasts and columns (Peters and Bork, 1998) support a diverse epibenthic community. Other factors possibly contributing to diversity include periodic disturbance by storms, and moderate productivity within the photic zone.

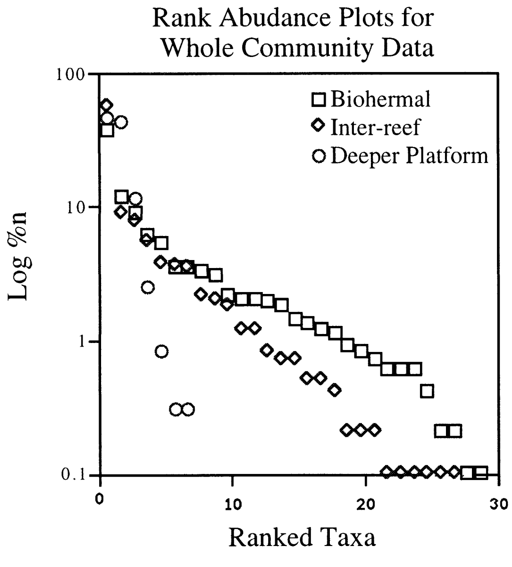

**FIGURE 5**—Rank-abundance plots for whole community data. Y-axis in percent number of individuals to facilitate curve comparison.

Microbioherms supplied habitat heterogeneity that probably contributed to log-normal distribution of non-strophomenid brachiopods in the Biohermal Community. Decline in biodiversity occurred at the depth limit of algae-constructed microbioherms. It is evident that many organisms exploited microbioherms because fossils, including tabulate corals, crinozoans, annelids, bryozoans, and brachiopods, are frequently found affixed in living position to microbioherms (Fig. 8). The relatively stable habitat provided by microbioherms not only was exploited, but was probably essential for the survival of several taxa, including *Eucalyptocrinites tuberculatus* and the large spiriferid brachiopod *Merisinia maria,* which only occur attached to microbioherms and skeletal tempestites in the Biohermal Community. Similar organism-organism interactions in a frequently disturbed modern marine environment have been described by Woodin (1978).

Log-normal distribution of the non-strophomenid brachiopod fauna in the Biohermal Community reflects environmental and ecological conditions that are consistent with sedimentological evidence and the paleoenvironmental conclusions of Feldman (1989). It is possible to predict many of the environmental parameters associated with a pedunculate brachiopod assemblage conforming to the log-normal model because the ecologies of the taxa are, in general, well understood. For example, resources cannot be a strictly limiting factor under the log-normal model. In terms of Waldron pedunculate brachiopod ecology, resources would have had to include stable attachment surfaces. Oxygen concentration also would have had to have been high, and sedimentation rates could not have been excessive in order to support a log-normal non-strophomenid brachiopod fauna. Because other taxa also exploit hard substrates and benefit from similar environmental conditions, abundance distribution of the brachiopod fauna could reflect larger-scale community characteristics.

When microbioherms disappeared in the Inter-reef Community, heterogeneity decreased and a less equitable log-series distribution resulted. Biodiversity in the Inter-reef was probably maintained, in part, by the substrates provided by *Eucalyptocrinites crassus.* When alive, the holdfasts (Fig. 9) and stems of *E. crassus* supported a diverse and abundant epibiota that included the rhynchonellid brachiopod *Stegerhynchus,* crinozoans, corals, annelids, and bryozoans (McGee and Watkins, 1994; Peters

**TABLE 2**—Shannon-Weiner index of diversity and goodness-of-fit test results for Waldron paleocommunities. S is species richness of entire sample, H is the Shannon-Weiner diversity index of entire community, E is the evenness of entire community, $\chi^2$ is the chi-square result for model fit to nonstrophomenid brachiopod fauna, df is degrees of freedom in test, p is approximate probability that model and data set concur; $p = P\{\chi^2 > \chi^2_p\}$, where $\chi^2_p$ is value from cumulative chi-square distribution.

| | | | | Log-Series Fit | | | Log-Normal Fit | | |
|---|---|---|---|---|---|---|---|---|---|
| Community | S | H | E | $\chi^2$ | df | P | $\chi^2$ | df | P |
| Facies A: Biohermal | 29 | 2.50 | 0.74 | 8.83 | 3 | 0.03 | 0.40 | 2 | 0.82 |
| Facies B: Inter-reef | 27 | 1.85 | 0.56 | 2.03 | 3 | 0.57 | 1.32 | 3 | 0.25 |
| Facies C: Deeper Platform | 7 | 1.13 | 0.58 | — | — | — | — | — | — |

and Bork, 1998). The abundance of *Stegerhynchus* in the Biohermal and Inter-reef communities (Table 1) is attributed to the brachiopod's ability to attach to upright crinoid columns, which not only expanded the number of suitable attachment surfaces but presumably provided a feeding position in the higher-velocity currents above the benthic boundary layer (Peters and Bork, 1998).

Feldman (1989) stated that substrate stability decreased and sedimentation rates increased in Facies B. These environmental conditions are consistent with a log-series distribution for the non-strophomenid brachiopod fauna of the Inter-reef Community. In many modern communities conforming to a log-series model, there are typically one or two limiting factors that affect species abundance. Log-series distribution of the non-strophomenid brachiopod fauna in the Inter-reef Community may be the result of a limited number of stable attachment surfaces and by the high degree of niche space that was pre-empted by *Stegerhynchus.* Trilobites, gastropods, *Fistulipora,* and other organisms not requiring a stable attachment surface probably maintained similar population sizes across the Biohermal and Inter-reef environments, even though their relative contribution was greater in the less-diverse Inter-reef Community.

In the deeper-water, possibly lower-oxygen environment of the Deeper Platform Community, which we correlate with Feldman's (1989) facies C, habitat heterogeneity was minimal and disturbance was limited to quiet-water sedimentation following storms (Feldman, 1989). Microbioherms, crinoid holdfasts and stems, and skeletal tempestites were not available as attachment surfaces; thus, uniform soft substrate predominated. Biodiversity in this environment was low, and strophomenid brachiopods were numerically dominant (Table 1; Fig. 4). Evenness

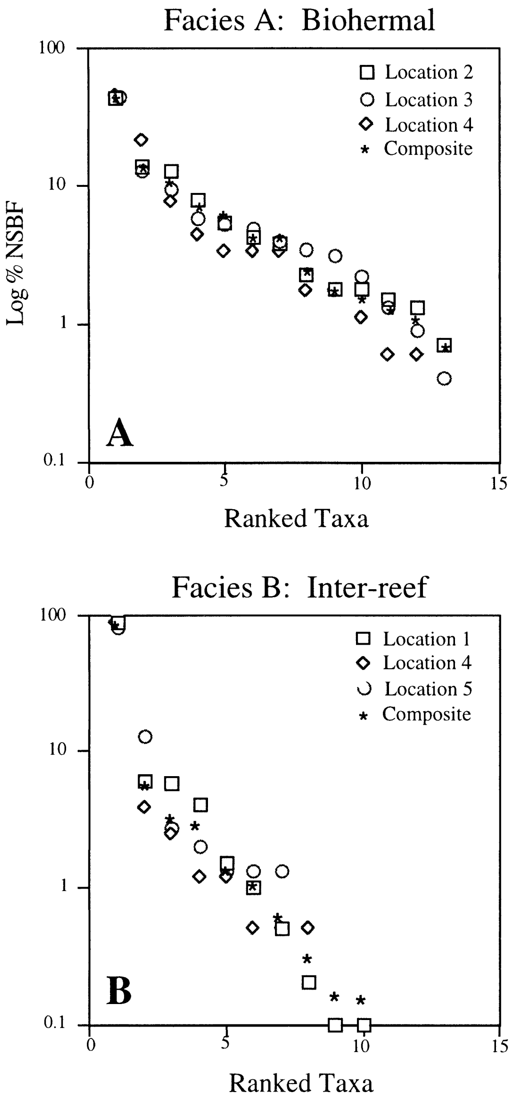

**FIGURE 6**—Rank-abundance plots for non-strophomenid brachiopod fauna showing consistency in species-abundance distributions at three localities. Y-axis in percent non-strophomenid brachiopod fauna (%NSBF) to facilitate curve-shape comparison. (A) Facies A: Biohermal Community. (B) Facies B: Inter-reef Community.

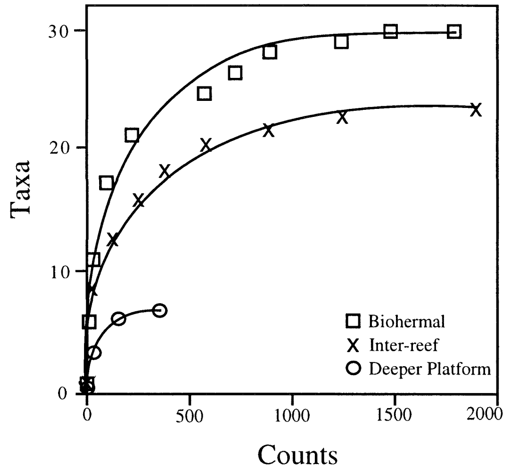

**FIGURE 7**—Number of taxa encountered as a function of number of field counts. Unsampled taxa include only rare species, indicating adequate sample size for rank-abundance analysis.

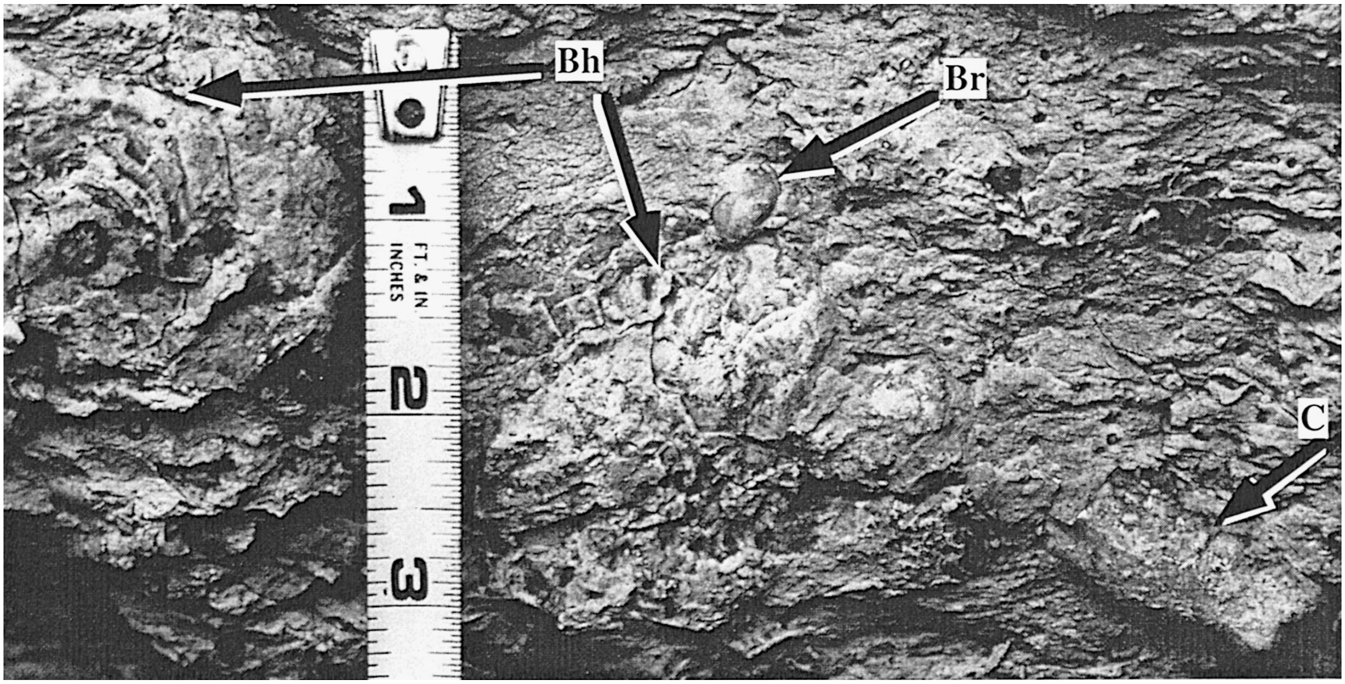

**FIGURE 8**—Cross sectional exposure of microbioherm in Facies A. A single *Whitfieldella nitida* (Br) is preserved in living position attached to microbioherm surface (Bh). An isolated *Eucalyptocrinites crassus* calyx (C) flanks the microbioherm and was probably deposited during the same storm event that buried the living brachiopod and microbioherm. Location 1. Ruler is in inches.

was quite high because of equitable allocation of abundant niche space to two strophomenid brachiopod species, one of which (*Strophochonetes novascotica*) had numerous spines on the hinge line that may have served as "mud-shoes" on a soft-substrate or as sensory devices during rudimentary swimming activity (Rudwick, 1970). Pedunculate brachiopods are rare in the Deeper Platform Community. *Stegerhynchus* may have attached opportunistically to small unpreserved algae mats (Archer and Feldman, 1986), and the few other pedunculate brachiopods encountered probably were transported into deeper water from the surrounding Inter-reef environment, and often are represented only by single valves.

Although too few species are present in the Deeper Platform Community to fit abundance data to a model reliably, the observed distribution of brachiopods most closely matches the broken stick. This distribution is most commonly found in communities where resources are shared rather equally among species. In the Deeper Platform Community, harsh environmental factors may have limited the number of successful species but offered plenty of resources to those few that were able to survive.

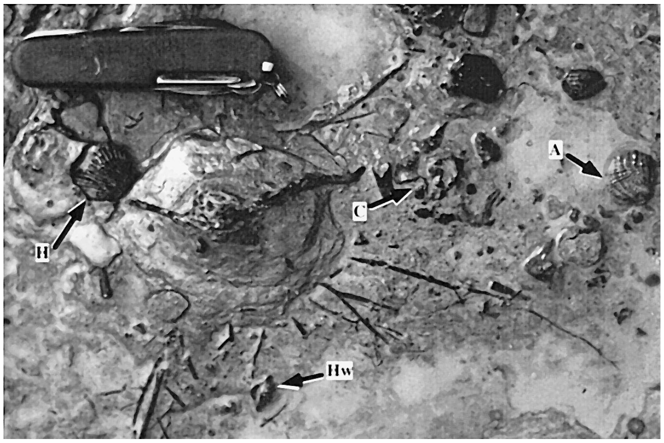

**FIGURE 9**—Bedding-plane view of branching *Eucalyptocrinites crassus* holdfast from Facies B: Inter-reef Community. Several brachiopod species, including *Homoeospira evax* (H), *Atrypa reticularis* (A), *Howellella crispa* (Hw), and *Stegerhynchus indianense* (C) are visible. Pocket knife is 8 cm long. Location 2.

### Summary of Community Replacement

Gradual environmental modification resulting from increasing water depth generated an ecological filter through which Waldron paleocommunities had to pass. Overall, the Waldron records deepening of the sea from above to below storm-wave base (Feldman, 1989), increased sedimentation rates (Shaver, 1996), and the loss of biodiversity through time.

Community reorganization in the Waldron involved several of the processes outlined by Miller (1986), including (1) expansion and contraction of the relative abundance of dominant species, (2) exchange of rank-abundance among less dominant species, (3) rapid demotion and promotion of minor taxonomic components, and (4) deletion of less abundant taxa. The Biohermal/Inter-reef reorganization occurred rather abruptly and is typically marked by a single bedding plane that, at least at one location, has extensive *in situ* preservation. Gradually changing environmental conditions were tolerated by important biotic elements perhaps until a threshold was

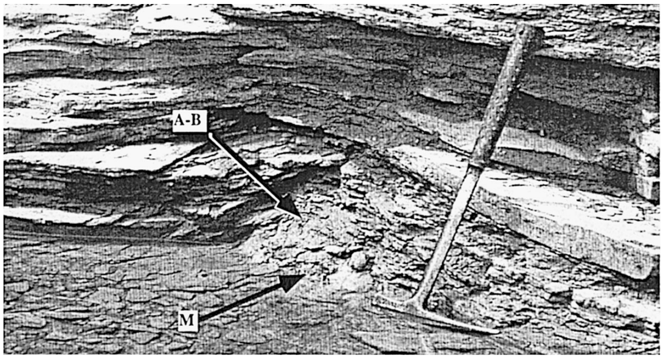

**FIGURE 10**—Outcrop view of top of microbioherm (M) in Facies A and overlying beds of Facies B. The Facies A-B boundary is marked by a bedding-plane surface (A-B). Location 2. Hammer handle is approximately 30 cm long.

achieved. Once the threshold of tolerance was exceeded, organisms and their co-dependents were removed from the community and a reorganization occurred. This was the case for the algae constructors of microbioherms and their associated epibionts in the Biohermal Community. The Inter-reef/Deeper Platform reorganization was more gradual, and was dominated by organism-environment interactions and longer-term promotion and demotion trends in the abundance of taxa as the environment uniformly and gradually changed.

### Defining Community Boundaries

Waldron paleocommunities were separated distinctly (Biohermal/Inter-reef) and on a gradient (Inter-reef/Deeper Platform). During early stages of Waldron deposition, the Biohermal and Inter-reef communities were juxtaposed laterally, but sharply separated by a depth-related physical boundary beyond which microbioherms did not occur. Because microbioherms were "villages" within which a number of epibenthic organisms lived, the physical boundary also marked a boundary between two co-existing communities that were composed of different taxa in different relative abundance. An easily visualized analogy would be a tree-line on a mountain side. For example, as altitude-controlled physical conditions dictate a change from ponderosa pine to lower-elevation communities, shifts occur downslope in species abundance. On outcrop, the boundary between the vertically stacked Biohermal and Inter-reef Communities is usually distinct (particularly at locations 1, 2, and 4) and often marked by a single bedding surface (Fig. 10).

In contrast, the Inter-reef and Deeper Platform Communities were neither distinctly separated vertically at a single location, nor separated laterally in a regional sense, but were part of a gradient. The Deeper Platform Community is present only in the deepest areas of the basin, presumably well below storm-wave base, possibly in relatively dysaerobic waters (Feldman, 1989). *Eucalyptocrinites crassus* was perhaps the most important community-structuring member of the Inter-reef Community. Crinoid distribution may have matched closely an environmental gradient (oxygen concentration for example) on the sea floor. Thus, no sharp physical boundary between the two communities existed, and a more continuous shift in taxonomic composition and relative abundance occurred with deepening water, as inferred from the sedimentary evidence.

Waldron paleocommunities, particularly the spatially well-defined Biohermal Community, appear to have been able to track their respective environments intact, as long as a relatively uninterrupted and continuous path was present between locations. This is evidenced by the high degree of community continuity between most locations. The southernmost Waldron Shale outcrop included in this investigation, however, was situated on the fringe of the local depositional basin, and was at a shallower water depth (meters to tens of meters shallower) than the locations to the north. When environmental conditions were established that allowed microbioherm development in the southern portion of the study area, only the algal elements from the northern locations succeeded in colonizing location 5 (Fig. 1). As a result, although general conditions were probably similar in the north and south, location 5 lacks the complete assemblage of invertebrates typical of the Biohermal Community. Only taxa capable of efficient dispersal or taxa that survived in suboptimal conditions presumably exploited newly opened environments away from previously established community locations.

### Implications

Organism-organism interactions were important in defining such Waldron community parameters as species diversity and the lateral distribution of organisms on the sea floor. Secondary tiering on upright crinoid columns was critical to the success of several epibiont species in the Inter-reef Community, where firm substrates were scarce. Patterns of relative faunal abundance were influenced strongly by this secondary tiering. In the Biohermal Community, scattered algae-constructed microbioherms were attachment surfaces for a diverse epibenthos, and organisms were concentrated in "villages" surrounded by soft, relatively unpopulated sea floor. Biotic interactions, such as those present in the Waldron, are known to be of importance in the modern realm, and may have been common in most Paleozoic communities. Surpassing threshold levels of environmental stress for key organisms also produced major effects on communities. Examples include the disappearance of microbioherms at the end of the Biohermal Community in response to increasing water depth and turbidity, and the gradual demise of *Eucalyptocrinites crassus* to mark the Inter-reef/Deeper Platform transition.

Species-abundance data for the non-strophomenid brachiopod fauna of the Biohermal and Inter-reef communities differ from one another and are congruent with existing models of abundance distribution. Empirical observation of modern communities has associated these models with general ecological conditions that may reflect certain environmental characteristics. In terms of pedunculate brachiopod ecology, the model-predicted environmental conditions for both communities are congruent with: (1) paleoenvironmental interpretations derived from sedimentologic, taphonomic, and paleontologic data; and (2) paleoecological conclusions drawn from field and specimen evidence. This implies that ecological models based on species-abundance can be applied to at least some Paleozoic benthic marine fossil assemblages, so long as the general ecology of the taxon used in the investigation is understood.

The Waldron Shale biota is well preserved and conducive to paleoecological investigation. Similarly preserved communities are rather rare but are present throughout the Phanerozoic record. These should be investigated in the field to determine community-environment interactions and congruence with species-abundance distribution models. However, completely preserved paleocommunities may not be a prerequisite for application of these models. If a formation is believed to preserve representatives of a particular taxon, the organisms can be used as "indicator species," even if the entire benthic community is preserved incompletely because of differential taphonomic or diagenetic loss. The preservation of at least some taxa in their appropriate relative abundance with respect to the living community may not be a taphonomically unreasonable expectation in many situations. Kidwell and Flessa (1996) have shown that biologically relevant information can be derived from many fossil assemblages, and that for many major groups, including benthic molluscs, most taxa are preserved in their appropriate relative abundance. Interpretation of species-abundance data, once obtained, would be dependent upon the ecology of the indicator taxon, and conclusions about communities would need to be considered in terms of the environmental factors relevant to the ecology of the indicator taxon.

Understanding local paleocommunities, at the outcrop and smaller scales, can reveal much about how biological communities respond to environmental changes. This approach more closely matches the spatial ranges of most modern ecologists, and also circumvents some Phanerozoic-scale biases in the fossil record at large; for example, outcrop area, number of researchers and interest level, and geographic distribution of studies (see Raup, 1972, 1976; Sheehan 1977; Signor and Lipps, 1982). Bambach (1977) tabulated the taxonomic richness of selected fossil assemblages throughout the Phanerozoic in an effort to determine patterns of metazoan diversification. Uniting data on Phanerozoic patterns in taxonomic richness (Sepkoski, 1993) and paleocommunity structure with knowledge of how diversity in individual communities responded to environmental change should help to identify important factors that control community structure and biodiversity.

Much of modern ecology lacks a geo-historical perspective. Hence, predictions about community fate in the face of environmental change tend to be speculative and without time-tested foundation. The Phanerozoic fossil record can provide modern ecology with tests of community response to environmental modification and can help give a temporal perspective, across a variety of scales, to some of the changes being observed in modern environments. Although there will never be one-to-one correspondence between a paleocommunity, its environment, and a modern ecological setting, understanding the large and small scale patterns of community dynamics from the Paleozoic to the Recent should form a solid foundation for predictive models pertaining to some aspects of community dynamics.

## CONCLUSIONS

(1) Waldron paleocommunities, defined by the temporal and spatial recurrence of taxa in similar relative abundance, correspond with paleoenvironments and their respective depositional facies as identified by Feldman (1989).

(2) Temporal and spatial boundaries between Waldron paleocommunities may be distinct (Biohermal/Inter-reef) or diffuse (Inter-reef/Deeper Platform). In each case, the boundary is defined primarily by the disappearance of community structuring biotic elements.

(3) Biodiversity decreases over time at each local section and across the depositional basin in response to third-order rise in sea level and other associated changes in environmental conditions (Fig. 2).

(4) Biodiversity is directly proportional to heterogeneity in the bottom environment. In the Waldron, calcareous algae microbioherms, soft-substrate rooted *Eucalyptocrinites crassus,* and skeletal tempestites contributed to habitat heterogeneity.

(5) In the Waldron, non-strophomenid brachiopods serve as indicator species that may reveal environmental conditions and whole-community characteristics in terms of the ecology of the group. Non-strophomenid brachiopods from the Biohermal Community fit most closely a log-normal distribution and from the Inter-reef Community a log-series distribution. Strophomenid brachiopods from the Deeper Platform Community approximate the broken stick distribution. Environmental conditions predicted by the models are congruent with conclusions arrived at independently.

(6) Waldron paleocommunities tracked their respective environments only when a nearly continuous path existed. Environmental barriers to community tracking, such as deeper water zones, were crossed only by taxa capable of living in sub-optimal conditions.

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# APPENDIX

## Location Information

1. Old Blue Ridge quarry, 2 km south of Waldron, Shelby County, Indiana. Waldron 7.5 minute quadrangle, NE ¼, sec. 6, T. 11 N., R. 8 E.
2. Quarry owned by St. Paul Quarries, Inc., Shelby County, Indiana. Waldron 7.5 minute quadrangle, SW ¼ NE ¼, sec. 4, T. 11 N., R. 8 E.
3. Quarry owned by Cave Stone, Inc., west of Norristown, Shelby County, Indiana. Hope 7.5 minute quadrangle, NE ¼ SW ¼, sec. 32, T. 11 N., R. 7 E.
4. Stream cut exposure near Anderson Falls State Park, Bartholomew County, Indiana. Grammer 7.5 minute quadrangle, NE ¼ SW ¼, sec. 12 T. 9 N., R. 7 E.
5. Walls of tunnel at abandoned mill, Jennings County, Indiana. Vernon 7.5 minute quadrangle, SW ¼ sec. 11, T. 6 N., R. 8 E.