Order Number 9009771

Community relationships of the Hamilton fauna of New York state: An application of community and hierarchical models and theories to paleoecology

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City University of New York, 1989

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COMMUNITY RELATIONSHIPS OF THE HAMILTON FAUNA OF NEW YORK STATE

An Application of Community and Hierarchical Models and Theories to Paleoecology

by

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A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philiosophy, The City University of New York.

1989

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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date

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Abstract

COMMUNITY RELATIONSHIPS OF THE HAMILTON FAUNA OF NEW YORK STATE

An Application of Community and Hierarchical Models and Theories to Paleoecology

by

Ron Pilette

Adviser: Professor Stanley N. Salthe

This work makes use of a hierarchical approach to describe Middle Devonian Hamilton assemblages as communities. Central to the study is the attempt to apply relevant neoecological models and theories to paleoecological situations. The study is based upon analysis of 107 sampling units and 132 species.

The descriptive component of the study relies upon multivariate analysis. Assignment of community types is according to robustness or corroboration. As part of this analysis, an evaluation of different scaling techniques is undertaken. For the sample evaluated, nothing abstracted further from actual counts than Percentages should be used. Deeper abstractions interfere especially in the identification of sampling units appropriate for use in structural and hierarchical analysis.

Seven community types are identified from the sample and are placed within the Hamilton paleoenvironmental model developed by Brett and Baird.

Population and community level contributions to structure are evaluated using a model developed by Levins and Lane. For the first time, this model is tested against Monte Carlo simulations. The existence of structure is determined and both population and community level contributions to this structure are found. The results are placed in the framework of Holling's stability-resilience model.

Finally, there is a direct empirical evaluation of hierarchical theory (especially as developed by Eldredge and Salthe). Levins's loop analysis model is used, and observed changes in population abundances are placed in Salthe's triadic framework. The result is a prediction in age structure (and accompanying size) changes for the dominant Chonetes in the community type evaluated. Preliminary testing supports the prediction, although not definitively, and invites further investigations.

ACKNOWLEDGEMENTS

A multifaceted study such as this is attributable to one person only because of institutional requirements. Of course all errors are my responsibility. However, there are many people to thank for encouraging and aiding me to err (and to be on the mark) in (at least to me) such interesting ways.

First of all, thanks go to the members of my committee: Niles Eldredge, Dave Franz, Les Marcus, Mike Novacek, and Stan Salthe. Each aided in their special way. My deepest appreciation goes to Stan Salthe -- ours was and is a special relationship.

My appreciation also goes to the outside readers: Carl Brett, Richard Levins, and William Miller, III. There are many others to thank, but I wish especially to name Gordon Baird, Peter Bretsky, Howard Feldman, Pat Lane, Robert Linsley, Linda McCollum, and Dave Schindel.

My last and continuing thanks go to Anna Vesely, my wife, for her intellectual and emotional support.

Financial aid was received from the American Museum of Natural History and the Geological Society of America in the form of student field work support. The City University of New York provided student travel and research funds. The Phi Beta Kappa Association of New York gave a generous award. I am thankful to each of these institutions.

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CHAPTER 1: INTRODUCTION

Purpose

If we are to understand the role that communities play in evolution we must initially understand more fully what fossil communities are. In addition, ecology will be a relatively more complete discipline to the extent that it includes relevant aspects of both neoecology and paleoecology. My study is grounded in these two postulates and is directed to the larger question of the role of ecology in evolution. If there is a discipline called evolutionary ecology which by definition and intent is reductionist in approach, there needs to be constructed a discipline, perhaps called ecological evolution, which is both reductionist and holist, thus hierarchical, in approach. This work asks the question: can we describe Middle Devonian Hamilton assemblages as communities using a hierarchical approach?

Proceeding from a multivariate-based community description, the core of the subsequent analysis derives from two approaches. The first is the use of the macroscopic measures of Lane, Lauff and Levins (1975). Theirs is one of the few studies attempting to search for macroscopic properties of ecosystems through use of biotic properties (McIntosh, 1985) and is perhaps the only community level method applicable to paleoecology. The second is a more directly hierarchical approach based on a particular use of loop analysis (Levins, 1975, Lane and Levins, 1977 and Puccia and Levins, 1985). The questions addressed are: Can we discover the lower level locus of change and show how to make predictions within Salthe's (1984 and 1985) triadic system? Can we begin to make the hierarchical approach an empirical one?

Finally, the Hamilton Group has received relatively little paleoecological study (Brett, 1986b). As Brett notes, this is surprising given the familiar and abundant fossils and the importance of the Hamilton in paleobiotic theory, i.e., the model of punctuated equilibrium as proposed by Eldredge and Gould (1972). There has, recently, been a resurgence of interest in the stratigraphy, sedimentation and paleoenvironment of the Hamilton (Brett, 1986a). However, the paleocommunity aspects of this work have generally been secondary to the stratigraphic and environmental work. My work attempts to redress this imbalance somewhat by focusing on the community problem itself.

A Brief Overview of the Hamilton

The Hamilton Group in central and western New York State represents a shallow arm of a broad epeiric sea in a tropical or near-tropical location which existed under generally stable conditions for 6 to 8 million years. There is a relatively full benthic marine fossil record.

1. <u>Stratigraphy</u>

Continuing investigations of the Devonian result in constant changes in the stratigraphy proposed for the period in terms of worldwide correlations and a more local Eastern North American basis (i.e., compare Rickard, 1964 and Rickard, 1975). Figure 1.1 represents an attempt to mesh Rickard (1975) with Harland, et al. (1982). The Hamilton Group is a Middle Devonian Givetian Rock Unit. It comprises most of the Cazenovia and all of the Tioughioga Stages. Figure 1.2 (adapted from Eldredge, 1972 and incorporating changes suggested by Baird 1979; Grasso 1986; and Brett, Speyer and Baird 1986) shows the division of the Hamilton into formations and members for central and western New York. The samples used in this study are taken from the Ledyard Member of the Ludlowville Formation and the Windom Member of the Moscow Formation. These formations are commonly referred to as the upper Hamilton.

The stratigraphy of the Hamilton is currently undergoing detailed reanalysis by Brett and Baird and their co-workers who have proposed numerous revisions. For instance, Grasso, Brett and Baird (1985) propose that the Swamp Road exposure in the Chenango Valley (see Rollins, Eldredge and Spiller, 1971 and Bailey, 1982) be placed in the Pecksport Member of the Marcellus Formation rather than in the Solsville or Bridgewater-Solsville Members of the Marcellus. Grasso (1986) has gone on to provide a redefinition of the Mottville. The value of such detailed reanalyses is seen, for instance, in Grasso's prediction that the "Mottville time-equivalent in the Catskill red bed facies should be found at or near the top of a regressive tongue, not a transgressive one". Despite these modifications, the classic work of Cooper (1930 and 1933-1934) continues to be the basis of stratigraphic efforts in the Hamilton.

2. Sediments

In central and western New York the Hamilton Group essentially consists of various types of shales and some sandstones and limestones (Fischer, Isachsen and Rickard, 1971). It is a "wedge of predominantly marine terrigenous sediment which thickens eastward" (Baird and Brett, 1983). It is underlain by the Onondaga limestones and overlain, unconformably, by the Genesee Group limestones and shales in western New York, and by the Tully limestones and black shales in central New York.

Within the upper Hamilton (Moscow and Ludlowville Formations) are numerous abundantly fossiliferous zones including widespread encrinites, complex shell beds, and coral beds (Brett and Baird, 1983).

The western to central New York upper Hamilton sediments are predominantly gray shales interbedded with thin limestones (Fischer, Isachsen and Rickard, 1971). The western New York "facies are replaced in central and eastern New York by siltstone and sandstone deposits. Fluvial sandstones and redbed floodplain deposits appear east of the Schoharie Valley" (Baird and Brett, 1983).

3. Paleoenvironment and Paleogeography

The Hamilton is located west of the Appalachian miogeosyncline whose timeframe covers the Late Cambrian through the Pennsylvanian. In the Appalachians, three principle Paleozoic mountain building events have been documented (Faill, 1985): the latter Ordovician Taconian orogeny, the Devonian (to Middle Mississippian? - Ettensohn, 1985) Acadian orogeny, and the Late Carboniferous to Permian Alleghanian orogeny.

> The clastic wedges of the miogeosyncline and foreland in both the Northern and Southern Appalachians suggest a like source -- deformed lands that were raised in the eugeosynclinal area as a result of plate impingement. This caused a reversal of the topographic relations of early Paleozoic time -- from a shallow-water shelf in the miogeosyncline area breaking off into a deep oceanic area in the eugeosyncline, into a highland area in the latter, which could shed detritus over the former shelf. The clastic wedges of different ages from one part of the chain to another illustrate the various plate collisions from place to place. (King, 1977)

The Acadian orogeny resulted in the raising of the lands to the southeast that were the source of the Devonian silici-clastic deposits. The orogeny is less clearly documented in the Southern Appalachians. The Acadian orogeny was apparently due to effects of the "rifting apart of crustal plates, and of subsequent plate collision (King, 1977)". These Acadian collisions appear to have occurred sequentially from north to south in the Appalachians (Faill, 1985 and Ettensohn, 1985).

The Hamilton Group is part of the Devonian clastic wedge which is more than 3000 meters thick in the Catskills, where its top layers have eroded, and thins to about 800 meters at the western edge of New York State. The wedge fans out from the Catskills, thinning westward and southwestward.

The Hamilton clastic wedge itself is approximately 975 meters thick in the southernmost Catskills and thins to about 80 meters at the western edge of New York State (Rickard, 1975). The Hamilton in New York represents deposits of the northern arm of a vast inland sea which covered a large part of Eastern North America (Cooper, 1957). The shelf and basin margin marine settings are recorded (Brett, Speyer and Baird, 1986). The more easterly deposits of conglomerates, red and green beds, and gray-green sandstones offer evidence of a nearshore and terrestrial depositional environment (Cooper, 1957). In New York, the sediments from east to west are indicative of a nearshore to offshore trend and result from the second Acadian tectophase in Ettensohn's (1985) Catskill Delta model.

Although it represents a stable shallow sea depositional area (the Acadian orogeny did not result in any major deformation reaching into the foreland basin -- Faill, 1985), the Hamilton deposits do not indicate an eventless or featureless setting. Regional subsidence occurred in the western Finger Lakes Region resulting in the separation of the stable shelf regions of the Buffalo Arch from central New York with the formation of thicker and/or anoxic deposits in between (Baird and Brett, 1981). There is also much evidence that during the Hamilton widespread (eustatic? -- see Johnson, Klapper and Sandberg, 1985) "transgressive-regressive cycles produced temporal shifts in litho- and biofacies belts normal to the margins of the Appalachian Basin" (Brett and Baird, 1983). Finally, there are many deposits in the Hamilton that are episodic in nature, including storm deposits that may have been laid down in a matter of hours to a few days (Brett, Speyer and Baird, 1986).

With respect to its setting in a worldwide context, the Middle Devonian strata of Eastern North America were deposited within a tropical-subtropical region south of the equator. At this time the continents were relatively close together, with the Avalon block sutured to Laurentia during the Acadian orogeny and only a narrow sea separating Laurussia from Gondwanaland (Seyfert and Sirkin, 1973; Bambach, Scotese and Ziegler, 1980; and Kent, 1985). Figures 1.3 and 1.4, which are reproduced from Brett, Speyer and Baird (1986), show the depositional setting of the Hamilton Group.

4. Paleontology

There is no single comprehensive source of information for the identification of Hamilton fossils. The Paleontology of New York series headed by James Hall and published in several volumes during the last third of the 19th century (Hall, 1867, 1879, 1884, and 1885; Hall and Simpson, 1887; and Hall and Clarke, 1888) is the most complete. Several hundred Hamilton species are identified and illustrated in these five volumes. "Index Fossils of North America" (Shimer and Shrock, 1944) describes over 200 Hamilton species. Rollins, Eldredge and Spiller (1971) provide comprehensive descriptions and photographs of a number of the Hamilton gastropods; Bailey (1982) illustrates bivalves; and, Ross (1953) illustrates corals. Finally, the American Museum of Natural History has most of these species within its collections.

Faunal lists are also available for various local areas and exposures. The "Geology of Erie County" (Buehler and Tesmer, 1963) is the most useful for western New York State and the "Paleontological problems of the Hamilton Group (Middle Devonian)" (Rollins, Eldredge and Linsley, 1972) for the Moscow Formation in the Chenango Valley. Lists are also available for various stratigraphic zones, such as Baird and Brett's (1983) compilation from two coral beds in western New York.

In total, there are approximately 800 described Hamilton species but many of these may be duplicates. Based on the above sources, Table 1.1 is a list of the major taxa found in the Upper Hamilton.

Samples

The sampling units (sensu Pielou, 1984) of the marine invertebrate fossils used in this study were taken from the Ledyard Member in western New York and the Windom Member in both western and central New York. Approximately one-half of the sampling units have been provided by Linda McCollum (1980) and another one-fifth by Carlton Brett (personal communication). I am deeply appreciative of both contributions.

The total sample is taken from field data of three different investigators. Therefore, for that portion of the analysis assuming equal rock volumes, adjustments to the raw data (based upon different rock volume samples) were necessary. Appendix 4.1 describes these adjustments.

Figure 1.5 and Table 1.2 show the location of the sampling units used in this study. Table 1.3 lists populations by sampling units and Table 1.4 characterizes the populations within successively larger taxonomic groups and according to trophic, mobility, and substratum relationships. Chapter 4 contains a detailed review and description of the sample.

CHAPTER 2: COMMUNITY ECOLOGY AND PALEOECOLOGY

The Nature of Communities

1. Concepts

Ecologists are by no means in agreement on a definition of the term "community": the very reality of communities is a debated issue. Much of the debate revolves around the issue of physical versus biological control. The lack of ascertainable biological interactions is often taken as prima facie evidence against the existence of a community. Simberloff (1980) chooses the population level for his approach and appeals to other levels (higher or lower) only if the "most parsimonious hypothesis, that species are individually distributed according to their interactions with their physical surroundings" is falsified. But, it would seem that it is precisely in such cases, where there is a corroborated correspondence between the physical environment and the distribution of particular species, that one might also find biological relations as well. "There is nothing inherent in the community concept which excludes physically determined boundaries" (Levins and Lewontin, 1980). If communities are considered to be essentially physically or biologically controlled, the possibility that they may be both doesn't often present itself to the investigator.

Hoffman (1979) and Simberloff, using parsimony as a primary criterion, both view communities as epiphenomena of population level interactions. Hoffman goes on to conclude that paleocommunity analysis has little to contribute to the "understanding of ecological interrelationships within natural communities". In addition, he believes that group selection would have to be demonstrated in order for the community assumption to be valid (Hoffman, 1979).

Levins (1975) presents us with an alternative view. Firstly, through his loop analysis model, he shows that group selection can, indeed, be at work in communities and that it may at times oppose Mendelian (Darwinian) selection. Secondly, he notes that a "formal manipulation of symbols can translate group selection into Mendelian selection, but such a manipulation obscures the significance of the processes involved. Parsimony is no virtue when it masks understanding" (Levins, 1975).

Historical reviews of the community concept by Whittaker (1962), Stephenson, Williams and Lance (1970), and Simberloff (1980) indicate clearly the influence of relatively extreme physical or biological control views. There is also the tradition, explicit at least since MacFayden (1963), that a continuum of concepts should be considered. Valentine (1973) notes five concepts placed in order of the increasing amount of organization required:

1. A living association of populations of species.
2. A recurrent association (space or time) of populations of particular species.
3. A recurrent association of populations,

> internally regulated to some extent so that it acquires a certain dynamic stability.
> 4. A recurrent, internally regulated association of populations containing integrative features that are more than simply a result of the collective properties of the population.
> 5. A recurrent, internally regulated association of integrated populations that forms a sort of superorganism.

Valentine dismisses the first concept as a truism and the last as possible only if selection can be shown to act between communities. Although selection is at least implicit in some superorganism views, the crucial issue is the process of succession (Simberloff, 1980 and McIntosh, 1985). Within this context, the superorganism view has been laid to rest by Gleason and his followers. Although Simberloff accuses some contemporary investigators of espousing a superorganism view through adherence to a multiple stable equilibria concept, it appears to me that this concept (only indirectly related to succession) can more usefully be seen as falling within the fourth community concept.

Valentine's second community concept suggests physically controlled communities. There are many adherents to this position, especially among benthic marine ecologists: (Petersen, 1918; Thorson, 1957; Johnson, 1964; Sanders, 1968; Boucot, 1981; Gray, 1981; and Paine, 1983). Many of these authors point out that their views are arbitrary and serve only as an initial assumption.

In the third concept, communities are biologically regulated through population level phenomena and adaptation to the environment is a strong factor. Valentine himself supports this concept of community. Many of the proponents of the second concept appear to also readily accept the third concept when they wish to acknowledge the biological role that might be seen to operate in communities. Hecht and Hoffman's (1986) argument for individual species response to "environmental challenges" is an example of the population level regulation of community concept.

As defined by the fourth concept, community phenomena are controlled by community level traits to a significant extent. More importantly, some of those who work with this concept claim that alternative views should not be mutually exclusive (Kauffman and Scott, 1976 and Levins and Lewontin, 1980). Accordingly, one would seek to measure various community attributes appropriate to concepts two, three, and four -- physical, population and community characteristics -- and seek to explain the relationships, if any, found.

Some physical characteristics appropriate to a paleoecological benthic marine study would include substrate, depth, temperature, salt ion concentration, oxygen, light, turbidity and storms (Boucot, 1981). Information of this kind would be gathered indirectly through stratigraphic and sedimentary descriptions including sediment grain size, external structures such as mudcracks and ripples, internal structures such as stylolites, rock type and color, rock composition (minerology and grain type), and bed thickness (Walker, 1969).

Macdonald (1976) has looked at population and community characteristics of marine benthic macrofauna. His population or component species characteristics are frequency, abundance (absolute, relative and rank), dispersion, fidelity, vitality (the "degree to which a species completes its life cycle within a single community"), periodicity, and adaptive strategies. Macdonald's community characteristics are taxonomic composition, equitability, species diversity, homogeneity (community "pattern"), species succession, trophic structure, standing crop and productivity.

2. Focus

Community studies can be classified as being either horizontal or vertical in approach. In paleoecology, horizontal or guild studies are directed at the relationships among populations found at the same trophic level (Sheehan, 1975 and Antia, 1977). The role of competition is often the focus of the study (e.g. Levinton and Bambach, 1975). A review of papers found in ecologically oriented journals or symposium books (e.g. Strong, et al., 1984) indicates the considerable significance in neoecological work of the idea that a single trophic level suffices for consideration as a community. In a review of Boucot (1975), Ager (n.d.) points out the "contradiction" of a community described as consisting solely of a single genus.

Vertical or cross trophic level work is also routinely undertaken. In paleoecology, vertically oriented studies include those of Walker and Laporte (1970) and Bretsky and Bretsky (1975). In neoecology, Herbold (1984) and Pimm (1984) provide examples of vertically oriented approaches.

In more inclusive approaches the roles of not only macrobiota but also microbiota and meiobiota are considered (Gray, 1981). Gerlach (1971) studied the meiofauna in a Recent sublittoral benthic community and found that, although they total up to only approximately 3% of the macrofauna biomass, considerations of metabolism show that biomass created is approximately 15%. Turnover rates were inconclusive, but are obviously important to understand. Wigley and McIntyre (1964) obtained similar biomass results: 3% to 8%. Walker and Laporte (1970) represent one of the few paleoecological attempts to incorporate meiofauna (beyond simply noting their presence) into an analysis.

In neoecological studies, concentration on horizontally or vertically defined communities is often related to the investigator's interest in showing the importance, or unimportance, of either competition (horizontal) or predation (vertical) in structuring communities. Whichever is emphasized, communities are defined and studied in accordance with one's research interests and are, in a sense, of secondary importance in the studies. An approach which takes communities as important in and of themselves is called for. In this context, both horizontal and vertical considerations could help us understand communities directly. Valentine's (1973) discussion of communities implicitly assumes such an approach.

Mills' (1969) working hypothesis is that "community means a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups". The definition is intended to be "practical" in the sense of opening up areas of inquiry rather than closing them off. If, by using this definition, we recognize that the physical-biological or population-community aspects are not to be construed as either/or possibilities and that we should consider communities within their own terms of reference, we might be in a reasonable position to study communities and their relevant phenomena.

Only by assuming that communities *might* be more than epiphenomena can we discover community level structure and processes of potential interest. Eldredge (1984) makes a similar point with respect to macroevolutionary phenomena.

3. *Description*

An important trend in modern paleoecology is the undertaking of Recent community-based investigations by paleoecologists. Among the many marine studies are those of Newell, et al. (1959), Johnson (1964, 1965, 1970, 1971), Warme (1971) and Macdonald (1976). Although the investigators do not always share the same interests, there is a general focus on taphonomic problems, especially in comparisons of live and dead assemblages. Macdonald concludes that "qualitative community attributes such as environmental setting, spatial and temporal distribution, and taxonomic composition are most likely to be accurately preserved". The environmental setting is constituted by the physical characteristics noted previously and its qualitative preservability can be assumed to be significantly probable from a review of the numerous paleontology studies that routinely establish environmental parameters. Reyment (1971) also notes the preservation of environmental setting. A possible exception to the list of physical characteristics is oxygen (and other elements). Researchers have found that elements in rocks are especially difficult to trace back to their origin -- a many-to-one problem (Levins, 1966).

Cyclic and episodic sedimentary events are important in and of themselves as paleoenvironmental characteristics (Duke, 1985). But, further, their very existence and close study of them helps the paleontologist to gain greater control of time and space in the fossil record (Schindel, 1980; Baird and Brett, 1981 and Einsele and Seilacher, 1982). The interpretation of paleo-storm events are in keeping with modern marine storm effects as observed by Hayes (1967) in studies of before and after storm situations, Reineck and Singh (1972) and Kumar and Sanders (1976).

Macdonald (1976) states that "Quantitative 'structural' community characteristics, such as taxonomic diversity, equitability, homogeneity, and trophic relationships (trophic groups sans energy flow), will be adequately preserved in some low-turbulence environments, but will become progressively less reliable under increasingly turbulent conditions." The extent of the retrieval of community level data is crucial to the possibility of an adequate evaluation of the biological roles in a community. Because of my choice of the subtidal part of the Hamilton for this study, there is a reasonable potential for observing and analysing the 'structural' community characteristics that might occur in the environment during the relatively stable time represented by the Hamilton Group. However, dynamic community aspects such as productivity and energy flow are not likely to be retrievable (Macdonald, 1976).

Macdonald also argues that paleocommunity studies should be restricted to preservable shelled taxa. Recognising the importance of soft-bodied organisms in ancient communities, he notes that shelled-taxa structure "may be quite different from those of the 'total community' to which they once belonged" (1976). Walker and Laporte (1970) have shown that it is possible to include soft-bodied fauna and meiofauna in paleocommunity analysis if one does so in a qualitative manner. A problem arises if one wishes to treat all the fauna in precisely the same way -- e.g., if all fauna are to be included in a calculation of equitability. In this case, equitability becomes the reified object of the study itself, rather than being a character for measurement that can help us gain insights concerning the community.

In my own study, there is by no means a resolution of the issues discussed above. I address physical characteristics in general for the sample location in time and space, drawing on the work of McCollum and Brett and Baird and their coworkers. Detailed physical descriptions and measures at the level of the sampling unit are not attempted.

On the other hand, a wide variety of population and community level characteristics (subject to the limitations discussed below) are investigated. A major limitation is that only macrofauna, and most often just shelled macrofauna, is included in the analysis.

Distinguishing community from population characteristics and characterizing each by use of a variety of tools, including multivariate analyses, will not resolve issues in the debate over the reality of communities. This section of my analysis, however important, is essentially descriptive. The issue of community reality can be addressed by either applying a set of measurements that can give results not meaningfully (or at least parsimoniously) explained by population level phenomena [the macroscopic measures of Lane, Lauff and Levins (1975) may be such a set of measures; a description and analysis of its use is given in Chapter 5] or making a successful prediction using a model based on community relationships [Turnover Rate prediction (Lane and Levins, 1977 and Puccia and Levins, 1985) based on loop analysis would be such a prediction; a description and analysis of its use is given in Chapter 6].

Community Characteristics

1. Trophic Structure

Macdonald (1976) separates trophic relationships from energy flow. Walker (1972) has separated trophic structure into trophic groups and food webs. Macdonald argues that trophic groups (his trophic relationships) are recoverable but food webs (his energy flow) are not. It may, however, not be possible to recover either.

A trophic group is a feeding type (after Turpaeva, 1957): either a swallower (infaunal deposit feeders), a collector (epifaunal deposit feeders, scavengers, and browsers), a low-level suspension feeder, or a high-level suspension feeder. According to this theory, a community is usually dominated by one such group and a dominance hierarchy locates each successive species as a member of a different trophic group. Supposedly, this hierarchical arrangement minimizes competition between and within groups. (A similar argument is used in support of tiering, the vertical distribution of organisms in space. The role and evolution of tiering has been addressed by Ausich (1980) and

Ausich and Bottjer (1982)). Trophic group analysis is considered to be especially useful in studying the abundant species and is, thus, of great potential utility in paleontology where these species are "most likely to have been preserved" (Walker, 1972). The quantitative relationships (for trophic group patterns) among preserved taxa are assumed to be broadly similar to those of the original community.

Walker analyzes the trophic group pattern for eight fossil communities. If the null hypothesis were applicable in this case, approximately 25% of the time (there are 4 trophic groups) the preceeding species in a dominance list should belong to the same trophic group, contrary to the expectations of the theory. Walker's overall value is 22% (13 of 59) and the value for the dominant is 25% (2 of 8). The results are nearly precisely what would be predicted to occur by chance. He offers some explanations for these results but they rely on the <u>assumption</u> of the minimization of competition. The theory, in fact, can not be falsified (Popper, 1959). Care must be used in evaluating trophic group results and such analysis should be used only in conjunction with analyses of other community characteristics.

Food webs cannot be analyzed quantitatively in the fossil record; however, if used carefully with other information and under the right circumstances, food web analysis can be tried as a qualitative approach with different degrees of confidence in different parts of the web. Olson (1966) has done this admirably in studies on the origin of mammals. It is obvious from his work that such studies are extremely complex and it is understandable that similar investigations have not been attempted.

2. Interactions

Competition is currently a heavily debated topic in neoecology (e.g., Strong, et al., 1984 and roundtable in The American Naturalist, 1983). Rather than evaluate the debate, I will focus on paleontological considerations. There are numerous fossil studies in which competition is offered as an explanation of the patterns observed (i.e., Levinton and Bambach, 1975 and Stanley and Newman, 1980). In the former study, the researchers examined particular horizontal communities in the Silurian and Recent, and concluded that competition was an important structural process in both.

Woodin (1983) has noted that it is generally impossible to "infer a mechanism (competition or predation) giving rise" to particular patterns seen in static examples from the Recent and Paleozoic. Essentially, the problem is many-to-one causality (Levins, 1966). There simply turn out to be several different processes or combinations of processes which could have produced a particular pattern.

Levins (1975) has shown that predator-prey relations will have different effects depending on the overall structure of the community. Barkai and McQuaid (1988) have documented a case of predator-prey reversal in a Recent benthic marine ecosystem. In his open system non-equilibrium model, Caswell (1978) has shown that competitors will "act as predators" in some situations. Competition and predation are not being denied as important biological controls. Rather, the effects of competition and predation are quite difficult to demonstrate in a variety of instances.

In light of the difficulty of interpreting particular communities, it is astonishing that Stanley and Newman (1980) found competitive exclusion to be operating between balanoids and chthamaloids over a period of 50 million years. In response, Paine (1981) noted that Stanley and Newman's evidence was inferential. Gould and Calloway (1980) found that the often described competitive replacement of brachiopods by bivalves in the fossil record could be explained by differential response to the Permian extinction event. Gould and Calloway went on to note that "passive extrapolation of microevolutionary theory into the vastness of geological time has often led paleontologists astray".

Ghiselin (1987a) has argued in support of findings of competitive explanations for patterns seen in the fossil record. However, he equates ecological competition to that of competition in human affairs and has reduced it to a theory that explains everything and therefore nothing in a meaningful way. If one measure of competitive success is related to "the consequence of effective predator deterence", then surely it is a measure that will never be made.

It would seem that paleocommunity analysis should take competition and predation into consideration without allowing the concepts to control the analysis. A potentially useful inquiry, for example, would be to examine the possible existence of refuges (Woodin, 1978) in specific paleocommunities and their effects on community structure (Woodin, 1983). It also should be remembered that the "consequences of one process [predation or competition] do not preclude another, or somehow require that they be ranked" (Jackson, 1988). Again, as with the issue of physical and biological control of communities, it is the either/or approach that is counterproductive.

Amensalism is another biological interaction that can have important community consequences. In a study of the Recent benthos, Rhoads and Young (1970) found that deposit feeders could intensively rework the upper layer of soft muddy bottoms. The resulting resuspended material in the water column could then clog the filtering structures of suspension feeders. Consequently, the numbers of suspension feeders would be decreased despite a good source of food. Obviously, the overall trophic structure would be affected.

Many paleontological studies note that particular lithologies have been intensively reworked. As a result, physical sedimentary structures are frequently obscured (Walker, 1969). Intensive reworking by deposit feeders is an example of the effects of an organism on its physical environment (Levins and Lewontin, 1985). Whether or not there were amensal effects in fossil situations as well is difficult to determine.

3. Larvae

My attention has been drawn to the importance of larvae in community ecology by Macdonald's (1976) consideration of "vitality": larval ecology is central to the concept of vitality. There is a considerable body of work on larval ecology but little deals with its effects on community structure. For example, Valentine (1973) discusses larval life because larval "properties are of considerable importance in determining adult living patterns", but he does not discuss larval attributes in terms of communities. Larval ecology for paleontologists seems to be limited to its role in generalized distribution patterns seen over geologically long periods of time (Hansen, 1980, Jablonski, 1982 and Valentine and Jablonski, 1983). Boucot (1981) in an encyclopaedic review of paleoecology does not mention larvae.

The difficulty of incorporating larval ecology into community work is underscored by the discussions of adult-larval interactions in Recent environments by Gray (1981) and Jackson (1983). One is left with a feeling of the formidable challenge of being precise in this area. Unravelling the role of differential larval ecology in paleocommunities, especially the structuring of communities, appears to be practically impossible. Differentiating planktotrophic and non-planktotrophic types at the fossil species level requires too great a use of analogy with Recent forms; members of the same genus may, in fact, be of different types.

4. Succession

Paleoecologists have paid a great deal of attention to succession; however, until very recently, the only complex theory of succession referred to has been the classical facilitation model. Johnson used studies of Recent benthic environments (1970, 1971) to formulate an approach to paleosuccession studies (1972) and concluded that shallow water benthic communities found "in a relatively constant general environment" are essentially controlled by the physical environment. We must also add another of Johnson's statements: "There can be no doubt ... that benthic communities do progressively modify their physical environment". What do we make of this apparent contradiction?

Johnson (1972) uses the term "constant general environment" to specifically encompass various environmental changes. Environmental changes (Johnson's physical control) downgrade a community into a typical species structure

(Johnson's mix of characteristic, intergrading and ubiquitous species). Classical facilitation succession can then take place in the absence of environmental changes and predictable changes in species structure will take place. Thus, Johnson has differentiated succession into two different levels of process. However, these levels do not refer to his "microsuccession" (species by species) and "macrosuccession" (community by community). The latter appears to include both responses to environmental changes and those points in classical succession when, in the absence of primary physical control, one community clearly replaces another.

Bretsky and Bretsky (1975) attempted to test Johnson's disturbance downgrading hypothesis but were unable to come to a clear conclusion from the analysis. The difficulty was due, in part, to their sampling techniques of Ordovician benthic marine assemblages. Essentially, they sampled every 25 feet vertically. By not controlling for gaps and by sampling arbitrarily in a succession study their discussion of mechanisms would be ad hoc. How is it possible to distinguish between succession and simple temporal and spatial replacement (Rollins, Carothers and Donahue, 1979)?

Walker and Alberstadt (1975) attempted a comprehensive successional study for a variety of samples including fossil reefs. They used the concepts allogenic (physically controlled) succession and autogenic (biologically controlled) succession, and followed Johnson in their approach to succession. Rollins, Carothers and Donahue (1979) criticize Walker and Alberstadt as they did Bretsky and Bretsky: for failing to distinguish between succession and simple temporal and spatial replacement.

Using their work on Pennsylvanian limestone communities, Rollins, Carothers and Donahue (1979) address the problem of techniques used for the recognition of succession in the fossil record. Their complex approach requires differentiation of the various successional effects of transgression and regression, high and low topographic relief, and progradation and eustatic control of transgression and regression. Their study aims at locating different communities in the stratigraphic record and at interpreting succession within a larger environmental framework (in this case, expansion and regression of epeiric seas). The investigators explicitly attempt to deal with community boundaries by advocating the use of the end-member concept and by arguing that boundaries will only be as "distinct as the associated environmental stress gradient". They criticize Johnson's microsuccession theory which requires acceptance of communities as open-ended.

The difficulty of community succession analysis is indicated in the following comments: Firstly, Rollins, Carothers and Donahue interpret Johnson as opposing the physical control model to that of classical facilitation in shallow water benthic communities. But Johnson uses both models, each for a different level of explanation, and argues only that physical control is of greater importance. Secondly -- in opposition to Johnson, Bretsky and Bretsky, and Walker and Alberstadt -- Rollins, Carothers and Donahue suggest that succession should be limited solely to autogenic situations. Rollins, Carothers and Donahue state that allogenic effects "primarily afford limitations to the degree and pattern of successional expression". If allogenic succession had occurred, we ought to see the higher order species shuffling effects (among characteristic, intergrading and ubiquitous types) posited by Johnson, and these have yet to be conclusively demonstrated. Allogenic succession may very well exist but it's discovery in either Recent or ancient situations is difficult because of the detailed wide-area (required to study differential recruitment of species types posited by the theory) information and controls necessary. Thirdly, the use of boundaries in succession studies has not been clarified. The end-member concept comes from lithologic work and it's use in succession analysis has not been specified. In addition, Johnson did not specify what he meant by communities being open-ended, an important omission because notwithstanding Rollins, Carothers and Donahue: communities may have boundaries and be open-ended -- they can show the hierarchical property of near-decomposability (Simon, 1962). (See below for further discussion on boundaries.)

McCall and Tevesz (1983) studied the possibilities of preserving a successional record in Recent soft-bottom marine benthic communities and discovered that mixing, differential preservation, and time-averaging would cause severe problems. In their review of paleosuccession studies, they found that all were wanting and they concluded that succession would "not likely be preserved in the fossil record and that the interpretation of some preserved patterns is problematical".

Given the conceptual issues and the difficulty of distinguishing between succession and temporal and spatial replacement, it is a considerable challenge to study marine benthic paleocommunity succession. One might despair of such a study being at all possible were it not for a recent study by Wilson (1985). But, in fact, the difficulties have not been cleared up because Wilson was able to take advantage of a relatively unique situation in his Ordovician hardground study: encrusted cobbles overturned while the organisms were alive so that the "stages of community development should still be preserved on the cobble surfaces". The succession observed followed that of the tolerance or inhibition model of Connell and Slayter (1977), an alternative to the facilitation model which has been favored by paleoecologists. Wilson found that "all species, including the late successional dominants, were present in the early stages of colonization".

Miller (1986 and Miller and DuBar, 1988) has interpreted succession-like patterns seen in the fossil record in terms of community replacement -- the substitution of one community for another over longer periods than can be accounted for by succession.

5. Diversity and Equitability

In his review and discussion of species abundance relations, May (1975) concluded that the broken-stick pattern is observed in relatively simple communities where "some major factor is being roughly evenly apportioned"; that the log series (and geometric series) represents "niche preemption" in relatively simple communities; and that the lognormal is a statistical result of more complex situations. May also demonstrated that the lognormal distribution agrees with the "bulk of pertinent field data".

Sugihara (1980), however, has shown that the canonical lognormal distribution is not a statistical artifact and that the distribution accords with his hypothesis of a "hierarchically structured communal niche" brought on by sequential and "complex random breakages involving the transition of several niche axes into abundance". The lognormal distribution is, therefore, at least at this time, found to possibly have some biological significance (May, 1984). Nevertheless, Harvey and Godfray (1987) have shown that a "canonical lognormal species-abundance distribution need not reflect a canonical lognormal distribution of resource use" and have thus put into question the possible biological causes of a canonical lognormal distribution.

Sugihara also points out that individual examples are statistically meaningless because "all fractional abundances are equally likely". Many studies, including Deevey's (1969) fossil foram investigation are therefore problematic. "Rather, to test the hypothesis it is neccessary to consider a distribution of values taken from many assemblages" (Sugihara, 1980), a methodology that can be readily employed in paleocommunity analysis.

In an extensive review of benthic marine data, Hughes (1985, 1986) concluded that the bulk of the data agrees with his "dynamics" model rather than with the log series or log normal models. The dynamics model assumes competition and open communities as distinct from the assumptions of the other models. The dynamics model also predicts more numerous abundant species than does the log series model and a greater number of rare species than does the log normal model (Hughes, 1986). The sampling units used in this study will be evaluated against the various proposed models.

6. Boundaries

The limits of a community, especially in paleocommunity studies, are usually assumed either to coincide with environmental gradients or to fall out from analysis of a great number of samples (Bretsky, 1970 and Lawson and Novacek, 1981 are examples of the latter approach as is this study). While Rollins, Carothers and Donahue's (1979) use of the end-member concept may be workable with fewer samples, delimiting communities has generally been done in a framework of multi-community and multi-environment analysis.

Boundaries may very well be related to biologic structure, at either the population or community level. (This relationship is an issue in analysis even at the provincial level (Sheehan, 1975).) Tools for evaluating boundaries which are relevant for single or few assemblage considerations and which are based on biological criteria are available in the neoecological literature (Levins, 1975; Allen and Starr, 1982; Conrad, 1983; and Salthe, 1983). However, each has its limitations. By means of a combined evaluation of two or more different boundary analyses -- a robustness (Levins, 1966) approach -- it is possible to derive the most information. Such a comparative analysis has been undertaken for simulations of communities with meaningful results (Pilette and Salthe, 1985). Realistically, however, it may prove to be impossible to use any of the above approaches for paleocommunity study. While some of the difficulty is explained by the fact that only one of the above approaches (Salthe's) was at the outset explicitly formulated to deal with boundaries, the chief limitation of all the proposals (except perhaps for that of Allen and Starr) is that they require rather detailed knowledge (if only qualitative) of the biological interactions involved.

7. Equilibrium and Non-equilibrium

Historically, ecological models have been equilibrium or near-equilibrium oriented, but non-equilibrium approaches are currently increasing in importance. Issues associated with equilibrium/non-equilibrium questions include stability/complexity and stability/resilience.

Equilibrium is related to stability and non-equilibrium to resilience (Holling, 1973, 1986). (An earlier and somewhat parallel discussion is Margalef's (1969) study in which he used the terms persistence, endurance and lability.) Resilience is related to the need for persistence and to the ability of a system to absorb changes (Holling, 1973). Random perturbations are more destructive in environmentally less variable areas where populations are less resilient but more stable. Accordingly, we would expect that the Hamilton sub-tidal community, which existed in a tropical and relatively unchanging environment, would, in general, be more stable than resilient. A partial explanation of the results of the structural analysis undertaken in Chapter 5 is attempted in terms of the relationship between stability and resilience.

The stability of large, complex, computer-generated systems is inversely related to complexity (Gardner and Ashby, 1970, and May, 1972, 1973). May (1972) found that "model multi-species communities, for given average interaction strength and web connectance, do better if the interactions tend to be arranged in 'blocks'". DeAngelis

(1975) showed that the "nature of interactions" is important and that stability is increased by adding specific kinds of complexity to his food web models.

Recently, Pilette, Sigal, and Blamire (1987b and in press) situated these findings within a biotic framework. Analyzing Delaware Bay estuary plankton communities by means of loop analysis, they observed that there was no distinctive relationship between stability and complexity at the community level. However, for 'populations', the less connected each was to the whole system, the greater the percentage of stability relationships of which the populations were a part. In addition to this inverse relationship between stability and complexity viewed from the population level, it was also found that several populations varied their role with respect to stability depending on the community context.

Caswell (1978) has suggested a perspective based on a continuum between non-equilibrium and equilibrium and, more importantly, the idea that both concepts are needed in the evaluation of a community. "Perhaps a community consists of a core of dominant species, which interact strongly enough among themselves to arrive at equilibrium, surrounded by a larger set of nonequilibrium species playing out their roles against the backdrop of the equilibrium species." The non-equilibrium species might be Johnson's (1972) intergrading and ubiquitous species. One wonders if they might not be at equilibrium themselves at a higher provincial level.

Similarly, Sutherland (1981) suggests that "evidence for stability and instability can be found in all communities", especially when they are observed over time or when the spatial scale is changed. Sutherland concludes that the "search for a relationship between diversity and stability is pointless".

Using biological data in the literature, Pilette (1989) has simulated the arguments of Sutherland and Caswell and has found that the populations of a community can be placed into three classes with respect to relative contribution to community stability: stabilizing, neutral and destabilizing. In addition, it was found that a particular population might be required in order to have a community and yet be a destabilizing entity.

8. Brief Overview

The above review of characteristics which appear to be important in community studies suggests some comments: Firstly, it is exceedingly difficult to evaluate community characteristics either in Recent or fossil assemblages. The usual paleoecological response is to call for more detailed morphological and autecological data (Johnson, 1964; Boucot, 1975; and Paine, 1983). Obviously, the collection of such data is useful, but, as useful, would be a better understanding of current debates about neoecological theories (Hedgpeth, 1977), the appropriateness of applying neoecological theories to the fossil record (Miller, 1986) and community analyses that do not preclude the possibility of discovering and acknowledging community level phenomena.

Secondly, there is a use for an approach which attempts to consider a wider than usual variety of concepts, while not forcing particular results from various parts of the analysis (see below). One must keep in mind that there is not a one-to-one relationship between process and pattern (Peterson, 1983).

Thirdly, the scale of approach has consistently been an important consideration in community studies. Depending on the number of populations included or the time considered, communities can be interpreted as equilibrium/non-equilibrium (Caswell, 1978) and/or stable/unstable (Sutherland, 1981). The very discovery of a community depends on geographic scale (Allen and Starr, 1982 and Yant, Karr and Angermeier, 1984) and number of species included in a study (Rahel, Lyons and Cochran, 1984). Given these problems of scale, how can we ever hope to use the analysis of various characteristics (even assuming they can be adequately described) to help us define and analyze communities?

As a partial answer, I suggest two points to consider. Firstly, greater clarity about what we are attempting in a piece of work and the extent of its possible contribution to ecological and evolutionary understanding. Communities are not unchanging complexes and the object of investigation is not the discovery of A community. As Levins (pers. comm.)

has noted with respect to boundaries, community description depends on geographic scale, time scale and the purpose of an investigation. If communities do exist, then a carefully sampled, described and analysed assemblage will undoubtedly be an abstraction (cf. Taylor's (1985) "apparent interaction" community matrix -- see Chapter 6) but an abstraction of something real. Secondly, as attempted in this study (see Chapters 5 and 6), to apply methodologies appropriate for ascertaining the existence of community level phenomena. If we can derive useful answers from community level questions, we can argue that this is because our sample is somehow related to a community. What that relationship is will be one of the goals of the study. Another goal will be to get a feel, based on the study itself, for the reality or unreality of communities (Feyerabend, 1962).

Taphonomic Problems

Some of the above discussion has included references to taphonomy, and I will now address the subject more specifically.

In studies on Recent death assemblages, Johnson (1964, 1965, 1970, 1971) and Warme (1971) argue that, for shelled forms, taphonomic bias is not a serious problem in marine bottom assemblage analysis. Their conclusion is probably viable if its limits are kept in mind -- determination of environmental parameters and taxa found. Other Recent death assemblage studies indicate the difficulty of preserving trophic data (Antia, 1977) and population structure (Kranz, 1977). Kranz found that, even when working with anastrophic (local catastrophic) burial, the organisms' differential ability to escape burial would be problematic. Differentiation of dead (recently) from the buried alive members of an assemblage was also a difficulty, especially when compounded by differential removal (his resilience time) after death.

We have learned from Recent death assemblage studies that transportation is not a really significant issue in relatively stable marine subtidal environments, however, other problems remain. Brett and Liddell (1978), working with Middle Ordovician hardground communities, discovered that "variable timespans of non-deposition" led to superimposition of different generations. They found that, by using "categories of differing preservational stages", some of the overlaps could be distinguished.

Time-averaging may well be the most significant issue in taphonomy with regards to community analysis although significant advances have been made (e.g. Einsele and Seilacher (1982) and the efforts of Brett and Baird which have importance beyond their immediate studies). Schindel (1980, 1982) has made important contributions to dealing with time-averaging problems. His resolution analysis approach suggests the functional interrelationship of three aspects of stratigraphic enquiry: temporal scope (total geologic time), microstratigraphic acuity (time represented in each fossiliferous sediment example), and stratigraphic completeness (the discrepancy between temporal scope and time span necessary to accumulate the same rock interval without interruptions) (1982). Schindel's strategy for accomodating "negative evidence left as gaps by shifting habitat conditions" is analogous to Eldredge and Gould's (1972) argument for accepting "stasis" as real in their punctuated equilibrium model.

Most important, perhaps, is Schindel's recommendation that time-averaging be taken seriously -- a recommendation given full consideration in the Hamilton work of Brett and Baird (1983). Reyment (1971) does not mention time-averaging in his quantitative paleoecology book. Boucot's (1981) book on benthic marine paleoecology is also not overly concerned with time-averaging problems, an omission severly criticized by Paine (1983). Paine notes that

> the heart of the (paleoecology problem) is ... temporal and spatial averaging of material. ... it seems obvious that the high variance associated with ecological interactions, the vagaries of recruitment, and the rampant non-linearity, all of which are most apparent in the view of the world as a series of interconnected patches, would partially or wholly disappear when averaged in time and space. ... If the paleontologist's 'community' is equivalent to several of the units recognized by an ecologist but integrated to form a single sampling unit, then chaos does reign. ... such integration also tends to isolate interpretive paleoecology from the mainstream of ecological thought.

Time-averaging is also at the heart of the problem in analyzing such processes as succession, predation, competition, colonization, etc. (Schindel's (1980) "rapid ecological processes"). Ecologically meaningful analysis of these issues is central to understanding the evolutionary significance of biological interactions such as the escalation of armaments as proposed by Vermeij (1987). Except for unique situations, anything more than the most general understanding of rapid ecological processes is essentially beyond paleoecology at this time.

Damuth (1982) has developed an alternative and independent method of paleocommunity definition based on the possible existence of community level structuring processes. In a study of terrestrial mammalian assemblages (both Recent and fossil), Damuth wished to learn whether or not the relative abundances of species in his fossil assemblages were representative of the living communities from which they were derived. Accordingly, he developed a model based on a log-log regression of relative abundance on body mass which gave a -.80 to -1.30 (95% confidence interval) slope for ideal unbiased Recent assemblages. Fossil assemblages could then be evaluated with reference to this slope value giving us a paleoecological application of allometry (Calder, 1984). As Damuth noted, his method represents an independent biological approach which can be combined with physical taphomic approaches and thus lead to "more specific questions about bias in fossil assemblages".

At this time, neither Damuth's nor any other biological approach is available for detecting bias in benthic marine assemblages. However, as described and analyzed in Chapters 5 and 6, the issue of paleocommunity "reality" can still be addressed with the careful application of models focusing upon community level phenomena.

CHAPTER 3: A HIERARCHICAL APPROACH

The Use of Hierarchy Theory

In a series of responses to questions about the value of a hierarchical approach in science, Patten made several useful comments (in Troncale, 1985). Essentially, he noted the dichotomy between the increasingly strong epistemological role of hierarchical work in ecology and its weak or even non-existent ontological and empirical functions. Patten, perhaps more than anyone else in biology and ecology, has used hierarchical concepts in his empirical work for years. Patten has concluded that it has not been of significant empirical relevance. Recently, Miller (in press, a) has called for an empirically focused triadic hierarchic perspective. Belsky (1987), without explicit appeal to the hierarchical tradition in theoretically based work, uses hierarchical considerations to criticize empirical work on the effects of grazing. Belsky notes the tendency of investigators to "confound" levels.

It is widely acknowledged that hierarchies are conceptual aids for categorizing phenomena, but their ontological reality remains dubious, as does their usefulness in empirical investigations. It is my interest in the value of hierarchy theory for an empirically based study (see Chapter 6) that makes it important for me to develop my views on hierarchy theory.

In light of these limitations current interest in hierarchies is bound to pass, but may cycle back into vogue again, as it has before, out of some vaguely understood epistemological necessity. There are, however, also more definite reasons to be attempting empirical work with hierarchies at this time. Recently, there has been an explicit focus on levels and scales. This is especially so for those ecologists and evolutionary biologists who are finding the more traditional reductionist approach restrictive for their understanding and explication of biological phenomena. Allen and Starr (1982) have noted the crucial point of understanding the scale of approach. Scale refers to rate of a given process rather than size (Allen and Starr, 1982; Miller, in press a; see also Salthe, 1985 re "cogent moment"). Eldredge and Salthe (1984), Eldredge (1984 and 1985), Salthe (1985) and O'Neill, DeAngelis, Waide and Allen (1986) have addressed the question of the kinds of levels and hierarchies to be dealt with.

Scaler hierarchy theory relates to the "interactions of phenomena of different scale" (Salthe, 1985). These scale differences give us our discrete but interacting levels -- in other words, near-decomposability (Simon, 1962), the minimal property of scalar hierarchies. In biology, we deal with nested scalar hierarchies. The components or entities of the lower level are included in or subsumed by the next highest level. Thus, the organism (phenome -- see below) is made up of cells. The example raises a crucial issue with respect to hierarchies -- their subjective arbitrariness. The organism could just as easily be seen as made up of organ systems, tissues, etc. We find that there are no objective criteria for choosing levels that are not observer-centered. A subject-object split is not anymore possible in a hierarchical approach than with any other approach. Those methodologies (e.g., logical positivism) which have attempted the split have floundered.

Pattee (1973) has argued that the fundamental problem of the hierarchical approach is to understand the origin and relation of levels of structure and levels of description. In a very real sense, any given hierarchy is both a structural and a descriptive hierarchy. Because of this descriptive component, there is a context to the above-noted arbitrariness when choosing levels (or connecting them). Human practice (e.g., science) results in certain levels being regarded as appropriate given particular interests. Acknowledging the historical contingency of this practice, there are, for example, for investigations in evolution only certain levels that are of descriptive and, thus, structural interest. Given the descriptive component, certain structures are taken to be "immanent" (Salthe, 1985).

In addition to scalar hierarchies, Salthe (in press) has developed the idea of specification hierarchies. While scalar hierarchies refer to levels of scale in terms of intrinsic rate of activities (cogent moment), specification hierarchies refer to the developmental path or "trajectory" of an entity. A given entity is found in a particular scalar level where it traverses (potentially) the specification hierarchy relevant to it. Entities in a specification hierarchy cannot be viewed in terms of near-decomposability or nesting. A gastrula neither interacts with the blastula from which it developed nor is it made up of blastulas. Historically, ontological questions have generally been the least well addressed in hierarchical work. Salthe's specification hierarchies represent an attempt to address ontological issues. Specification-framed development differs from scalar development in that the former represents a view of development within a historical (evolutionary) situation while the latter represents a view of development at a given moment (see below for further discussion within the context of the Functional hierarchy and self-organization).

In this universe -- the only one we know of -- and from our human-centered perspective -- the only perspective we are capable of -- we are held to making statements about nature within a limited range of possibilities. There is required an assumption of an objective world (Sartre, 1976). A sincere skeptic would be completely paralysed because any human activity, even discourse, assumes the acknowledgement of something other than the self -- of the world. In addition, the subject is part of the world and thus cannot stand removed to learn about it objectively (e.g., von Uexkull, 1926, Sartre, 1966 and 1976, and Allen and Starr, 1982). Rather than attempt the impossible and arrogant task of abstracting ourselves from the world in order to learn about it, we must work with the world realizing the limits imposed by our membership in it. Of course, these limits may in fact be possibilities (or, a privilege -- Miller, pers. comm.): one wonders if the extent and pace of our environmental destructiveness would be the same if we fully realized and felt that we have a position in the world.

Unavoidable human subjectivity has implications for any hierarchical method: it must be human-centered and organism related (Eldredge and Salthe, 1984). The transferal of the initial viewpoint to another level, e.g., the cell, gene, ecosystem, would require a series of assumptions and abstractions in order to set the observation to the new level. These mental machinations are far more problematic than the need to properly evaluate the new level's phenomena in terms of the real level of observation -- namely, ourselves. We also would need new tools to discern how the viewpoint transfer might be made.

Which levels, then, do we choose? The initial choice is related to the questions that interest us and is, in a sense, a social production. For example, perhaps related to increasing awareness and concern over large-scale pollution, more ecologists and chemists are becoming interested in regional and biospherical level issues. Having made the level choice, we are well within hierarchy theory. Surfaces or boundaries (Allen, O'Neill, and Hoekstra, 1984 and

Salthe, 1985) become important considerations. Assuming the ever-present observer-centered methodology, some approaches to establishing boundaries are, nevertheless, more useful than others (Canny, 1981). In particular, evaluating the degree of congruence of independent approaches in a search for robustness across various criteria (Levins, 1966 and Wimsatt, 1980b) is important. For example, Pilette and Salthe (1985) -- in simulations of community boundaries -- found the criteria of robustness to be useful in suggesting appropriate boundaries.

Choosing Hierarchies

Eldredge and Salthe (1984) used solely Genealogical and Ecological hierarchies in order to reduce the descriptive complexity in a theoretical argument for the need of a hierarchical perspective and to lend as equal an emphasis to ontological issues as to economic ones.

Eldredge (1988 Blacksburg and manuscript) argues that both the Genealogical and Ecological hierarchies are best viewed in terms of relevant processes involved. He seeks to distinguish between reproductive and economic "attributes" or processes. This leads him to make the distinction between genealogical sexual selection (developed in the context of Paterson's (1985) Specific Mate Recognition System) and ecological natural selection for organism (phenome) level processes. Mishler (1988 Blacksburg) makes the useful point that the reproductive context needs to be further developed so as to incorporate asexually reproducing organisms as well. Eldredge maintains this dual process perspective in discussing other levels for both the Genealogical and Ecological hierarchies.

This contrasts with Mishler who considers the Genealogical hierarchy mainly from the perspective of patterns. This emphasis upon patterns is problematical for two reasons: Firstly, a pattern perspective is in danger of reducing hierarchy theory to the previous historical tradition of being essentially just an aid for categorizing phenomena. Secondly, any interaction between genealogical and ecological entities needs to be viewed in terms of process and much stands to be lost in potential understanding if genealogically based processes are left out of consideration. Mishler, in fact, does not leave these out of consideration (at least, not fully). They return via his ecological Gene Flow hierarchy (see below).

In the process of collapsing the abiotic and biotic into the Ecological hierarchy, communities (my special interest in this study) were lost. Eldredge (1984) focuses upon either the community or the 'local-ecosystem' depending "upon whether or not the abiotic realm is explicitly incorporated into the system". In Salthe (1985), a portion of the community concept is transformed into the genealogical "historical biota" (coevolving species).

Paleoecologists and neoecologists regularly make a series of abiotic determinations in their studies. In empirically focused work, where a distinction between living and non-living systems might be thought important (a distinction not always made in systems ecology), it would be simpler to separate the abiotic and biotic descriptions. This separation allows one to avoid the problem of having different 'kinds' of entities in a given hierarchy (Damuth, pers. comm.). Enzymes, cells, populations (Damuth's avatars, 1985), communities, etc. are examples of ecological kinds of entities while inorganic molecules, regolith, rocks, etc. are examples of abiotic kinds. Another set of similar kinds would be that of function circles (the relevant or meaningful environment) and their constituent entities of the organism (von Uexkull, 1926), local-ecosystems, biogeochemical surface of the earth (Vernadsky, 1949 and Lovelock, 1979), etc. which are examples of combined genealogical, biotic, and abiotic kinds, i.e., functional kinds. The distinction allows for a consistent definition of hierarchies <u>with respect to</u> the kinds of entities <u>within</u> a given hierarchy and, thus, satisfies the isomorphic (similarity with respect to governing laws and regularities) criterion for within hierarchical work (Simon, 1973 and Troncale, 1986). If the distinction of 'kinds' was not to be related to a distinction between living and non-living systems, then a single Ecological hierarchy based upon dissipative structures (Salthe, manuscript) would suffice.

Mishler (1988 Blacksburg) argues for breaking down the Ecological hierarchy into four hierarchies: Developmental, Ecological, Selective, and Gene Flow. It is based upon emphasis on different processes. The Developmental is concerned with issues related to Salthe's (in press) specification hierarchies. The latter approach is based upon the developmental trajectory of an entity largely <u>within</u> its particular scalar location. Mishler misses this important distinction. The Gene Flow and, to a certain extent, the Selective hierarchies are perhaps best viewed in terms of the processes relevant to the Genealogical hierarchy as developed by Eldredge (1988 Blacksburg and manuscript). Because Mishler has de-emphasized process in the Genealogical hierarchy, he has been forced to locate genealogically-related processes elsewhere.

Like Mishler, I feel there is value in an expanded list of hierarchies. However, I see a need for a basic isomorphism with respect to entities <u>within</u> a given hierarchy. While respecting the contribution made by the emphasis on understanding different levels and types of processes as developed by Eldredge, Salthe, and Mishler, an equal consideration needs to be given to entities -- the actual constituents of hierarchies and the <u>things</u> of the world.

From an overview of past uses of hierarchies (see the historical reviews in Eldredge, 1985 and Salthe, 1985), it is clear that the number of possible hierarchies and the particular levels chosen have been based on many different criteria. My purpose is to determine whether or not an empirical, community-oriented study can be usefully embedded in hierarchies. It is, therefore, not surprising that I have selected a particular group of hierarchies suitable to my interests. Specifically, I have made a distinction between genealogical, ecological, abiotic, and functional entities. The empirically addressed ecological community entity must be clearly distinguished from the relevant abiotic considerations and functional local-ecosystem. One important reason is that the triadic approach (Salthe, 1985), used to give context to the loop analysis technique discussed and evaluated in Chapter 6, requires that the upper level boundary to the population be the community (the lower level boundary being the organism -- phenome).

It is also necessary to relate levels in different hierarchies to one another appropriately. The local-ecosystem is at the 'equivalent' level of several phenomena in that it consists of an ecological community and appropriate abiotic entities, none of which are nested within each other. All these kinds of entities simply represent different focal points for quite different processes and phenomena of the same relative scale (and thus fall into different hierarchies).

We understand the relationships among levels in the abiotic realm even less than those within other domains, as is indicated by our classification of abiotic phenomena into two broad categories: element-oriented entities (e.g, inorganic nutrients) and process-oriented entities (e.g, climate). In ecology, this classification has resulted in the reduction of the abiotic realm to generalized matter-energy statements (see Odum, 1971, for a series of hierarchies with the Abiotic hierarchy treated in this manner). Much of what is called 'ecosystem' analysis is perhaps more usefully thought of as regional abiotic analysis (e.g. watershed studies) coupled with ecological considerations. That material flows link ecological and abiotic entities does not obviate the fact that broadly different processes are involved: one, adaptation and other life processes, and the other, purely chemical-mechanical responses. Analyzing a biogeochemical cycle within a hierarchical framework would necessarily involve different levels and different hierarchies unless we wished to approach it solely in terms of dissipative structures. If, as Findlay (1984) suggests, we gave matter equal billing (perhaps through emphasis upon the thermodynamic commonality of dissipative structures) to "conscious Spirit" we might be better capable of categorizing these thoughtless "noncaring" entities.

In Chapters 4 and 6, I treat abiotic considerations in a generalized manner rather than specifically for each community type, or, more importantly, each sampling unit. If I were to be more specific, the entity of interest would have been the local-ecosystem rather than the community.

The community orientation is a matter of both acknowledging the limitations of working with the fossil and rock record and a preference for the analysis of community properties.

Four Hierarchies Scheme

In my view, there are generally four hierarchies to be taken into consideration for studies involving living systems: Genealogical, Ecological, Abiotic, and Functional (see Table 3.1).

The distinction between genealogical and ecological entities is based on Hull's (1980) distinction between replicators and interacters which is based in the traditional dichotomy of fertility and viability components of selection. (Eldredge's recent distinction between genealogical and ecological organisms based upon sexual and natural selection processes represents a placement of the fertility component of selection in other than its natural selection context -- again focusing on a problem that has been with us since Darwin and is not resolved by Hull's distinctions.) Three precise definitions of Hull's (1980) are useful here:

> replicator: an entity that passes on its structure directly in replication
>
> interactor: an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential

selection: a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them (Hull, 1980)

In the development of hierarchy theory in this decade much clarity has been achieved by linking the Genealogical hierarchy to replicators and the Ecological hierarchy to interactors. With this in mind, I will very briefly note some relationships between various hierarchical efforts. Earlier work by Teggart (1925), Wright (1964), Valentine (1968), Bonner (1969), Miller (1978) and Bunge (1979) proposed single hierarchies. All, except Bonner and Miller, mixed genealogical and ecological entities together. Conrad (1976) and MacMahon, et al. (1978) produced single-forked hierarchies in attempts to distinguish between genealogical, ecological, and (in the case of MacMahon, et al., 1978) abiotic and functional entities.

A useful language for making the various distinctions -- genealogical, ecological : replicator, interactor -- was not available and, perhaps, more importantly, the need for separate hierarchies based on the distinction between important processes was not seen as needed at the time. Eldredge and Salthe (1984), Eldredge (1985) and Salthe (1985) have provided much of the needed clarity by proposing the linkage of genealogical to replicators and ecological to interactors.

The Ecological and Abiotic hierarchies have much in common. Both consist of entities which develop rather than evolve, exert selective pressure, are subject to the four basic phenomenological regularities of information and thermodynamics (Salthe and Pilette, 1986 and Salthe, in press), and interact so as to allow genealogical replication. However, only ecological entities can function in levels of selection in an evolutionary sense (Brandon, 1984 and Hull, 1984). The commonality of processes relevant to ecological and abiotic entities, and their interpenetration, should not obscure the fact that ecological entities are examples of matter-in-life and abiotic entities are examples of matter-'around'-life.

The fourth distinct hierarchy is the Functional, which encompasses the others (and their processes), such that the 'emergent' property of life is seen in these functional entities directly and fully. There is no such entity as a species, cell, community abstracted from its relevant function circle. A horse out of its environment will be in a vacuum and will be dead within five minutes of the 'abstraction'. With respect to establishing biologically relevant hierarchies, we need one hierarchy where life can take place at each level. This is as important for understanding the origin of life as well as its history and for understanding the specification as well as the scalar hierarchy. One property required by original living substance was the ability to affect its immediate environment -- to incorporate it into a function circle. Even the abiotic entities, from our biological perspective, must be either embedded or potentially embedded in a function circle. Otherwise, they may as well be in another solar system.

Patten's (1982) concept of the "environ" representing the organism and its relevant environment represents the function circle at the level of the organism. Bigger and Bigger (1982) use the concept of the "recognized" or "meaningful" environment of the organism. Odling-Smee (1988 and manuscript) discusses the "tolerance space" of the organism and population. This space is the source of immediate inputs and the sink for immediate outputs. Jackson (1987) represents a somewhat contradictory search for "volumetric objects" that include the natural space around organisms and smaller scale biotic entities. Von Uexkull (1926) has a relatively rich concept of functional entities, even if not extended to all such entities, and the term "function circle" was first used by him (see below for further discussion on function circles).

Thus, the Genealogical, Ecological and Abiotic hierarchies carry no additional burden other than being logically consistent with respect to processes attributed to their constituent entities. It is at the organism level that Eldredge and Salthe (both with some misgivings) appear to be inconsistent with respect to the genealogical-replicator and ecological-interactor distinction. This would allow a kind of privileged status for the organism to creep in -- something that the history of work in hierarchy theory is at pains, at least in principle, to try and avoid.

A distinction needs to be made between the necessarily human-centeredness of the hierarchical approach and the granting of privileged status to the (human) organism regarding the hierarchically-based rules of operation or processes. In this sense both the epistemological orientation of Allen, O'Neill, and their co-workers and the ontological orientation of Eldredge and Salthe need to be kept in balance.

Eldredge, especially, has insisted on our recognition of the replicative and interactive aspects of the organism. Locating the organism in the Functional hierarchy allows this dual recognition while preserving for the Genealogical and Ecological hierarchies organismic processes that are consistent with those seen at other levels of the respective hierarchies. Following this, genome (as used here) refers to the informational (hereditary and "daily" genetic) constitution of the organism (Conrad, 1983) and phenome refers to the economic (morphological, physiological, and behavioral) constitution of the organism.

Eldredge and Salthe, in treating ecological entities at the community or local-ecosystem level, especially, and, to some extent, higher ecological levels, tend to intermingle ecological and abiotic aspects. In lower ecological levels this mixing is not done. This is where Hull's third definition -- that of selection -- may be useful. I would argue that it is appropriate to make the distinction between entities that can <u>in principle</u> act as the economic locus of genealogical information in an evolutionary sense (ecological) and those that can not (abiotic). Ecological entities possess properties that enable them to be interactors in a selective sense -- they operate as levels of selection (Brandon, 1984 and Hull, 1984). Abiotic entities are capable of being interactors but not of playing this selective role. Both exert selective pressure however. Thus, I am making a distinction between a level of selection (or locus) and selective pressure (or context).

I would offer the following distinctions:

genealogical	ecological	abiotic
replicators	interactors	interactors
units of selection	levels of selection	------
------	sel. pressure	sel. pressure
evolution	development	development

I would also argue that when one feels the need to step outside of these distinctions, then it is necessary to move explicitly to the Functional hierarchy and consciously interrelate the various processes (tied to the various abstracted hierarchies) in a discussion concerning the full living entity.

Breaking the Abiotic hierarchy down into the three phases of gas, liquid, and solid may enable us to get a hand on this most elusive of hierarchies. The distinction between element-oriented entities (e.g. local metal concentration) and process-oriented entities (e.g. climate) makes an unwarranted distinction -- based upon supposed scale distinctions -- between matter and energy. Climate is just as material a phenomenon as local metal concentration.

In this case it is a scale difference that is crucial and it is scale distinctions that are the sine qua non of scalar hierarchical investigations. For example, global climate patterns involve relationships at a high level between the three phases in the form of oceans, land masses, and air masses. Similarly, in evaluating the effects of heavy metals on soil processes, it would be important not only to know metal concentration but also the proportion present in the water, air space, and regolith.

For the local-ecosystem, local abiotic considerations are important. For example, for terrestrial systems, land form (mountain, valley, flat land), exposure to sun, degree of aridity, movement of air mass, inorganic nutrients, etc. are all important considerations. The differential response of populations and the degree of incorporation of the local abiota into the function circle of the local-ecosystem all have an effect on this particular type of abiotic entity, which itself has effects upon other entities. A polluted nutrient source on the side of a hill may reduce and/or damage plants and animals which will then return less material to the soil. In this situation, erosion will increase. These kinds of relationships and interpenetrations hold for healthy systems as well.

Levels, as I have noted above, are generally chosen according to particular interests and capacities. The process of choosing is similar for hierarchies. The content of any aspect of the Genealogical hierarchy (other than the

Linnaean classificatory taxa) was not envisioned until about 130 years ago, and various entities of this hierarchy were first usefully characterized less than 90 years ago. Within the past 40 years and coinciding with the rise of molecular biology, an expanded list of the entities of the Genealogical (and Ecological) hierarchy has been developed. The significance is that our working list of hierarchies and the levels within them are historically contextual and change over time.

The Functional hierarchy is less of an abstraction from the LIVING, FUNCTIONING EARTH as we perceive it than are the Genealogical and Ecological hierarchies. The latter two only persist because they interact, along with the Abiotic, within the Functional hierarchy. Because the Abiotic forms and informs the Genealogical and Ecological, a reductionist logic is suggested although we still have no reasonably full description of how the organization seen in the Genealogical and Ecological hierarchies is determined by abiotic properties. However, the Functional is equally and necessarily formed and informed by the Abiotic, Ecological, and Genealogical. Consequently, any functionally focused study probably will have to break its data down into the categories of the other three hierarchies before attempting to pull them all together into a synthetic whole. It is here that Eldredge's (1979) "scenarios" may be appropriate, albeit developed from the more strictly systematic perspective for which the concept was originally derived.

It is this Functional hierarchy where the combined processes of Salthe's scalar (evolution/development) and specification (development-in-history) hierarchies interpenetrate and where self-organization becomes possible (see below).

Of what significance are these considerations for this study, the focus of which is ecological entities? My aim is not to synthesize. Rather, it is necessary to specify at the outset what a community, population, and phenome are, and to distinguish them from genealogical and abiotic elements as well as from the adjoining ecological levels.

Caswell (1978) has said that a community might be thought of as consisting of a core of equilibrium populations and a series of non-equilibrium populations. If Caswell is correct, then the equilibrium core could possibly represent the genealogical historical biota (Salthe, 1985) undergoing co-evolution -- in other words, we would find an aspect of 'community' evolution (Valentine, 1968 and 1973). The full ecological community could be looked at in terms of community succession (or development) because the non-core populations would be crucial here (see Chapter 2 for discussion of Johnson's (1972) three population types in this regard).

Only by means of a hierarchical approach is it possible to separate out the several processes involved in the various models and perspectives of which Caswell's is an example. Other discussions are clarified within the context of a hierarchical perspective. For example, Laporte (1979) reviewed trophic analysis and concluded that trophic classification and taxonomic classification were not particularly related. There are many examples of unrelated populations with identical food requirements and relatively closely related populations feeding in different ways. We would expect an ecologically functioning community to consist of certain trophic types with a variable mixture of the genealogical types permissible because a finer grading of our Ecological hierarchy would show guilds and trophic types interspersed between populations and communities.

Issues in Hierarchical Theory

1. Hierarchies and Individuals

The hierarchical concept would be only of heuristic value without the notion that levels are composed of individuals. Ghiselin's (1974) argument for the extension of the concept of the 'individual' to levels other than the organism has been the foundation for subsequent epistemological and ontological arguments. While the extension of the individual concept has a prior history (see Eldredge, 1985), Ghiselin has set the logical terms of reference. Individuals, as distinguished from classes, are necessarily, rather than arbitrarily, coherent. Individuals do not have members or instances (Ghiselin, 1974 and Hull, 1980) but they are spatiotemporally bounded (Hull, 1980). Eldredge's (1985) query about why Hull (1980) faulted the use of hierarchies in traditional biology perhaps can be answered by noting that previous efforts confounded individuals and classes in their hierarchies (in addition to the above-noted mixing of different kinds of entities) thus undermining even the heuristic value of the hierarchical concept.

There are problems with the individual-versus-class distinction. One issue is whether something is an individual or class based on our approach and questions. (Similarly, the distinction between development and evolution is to some extent based upon descriptive interests (Salthe, in press)). Ghiselin (1987b) argues against this, noting, for instance, that species "function as individuals in the processes that go on in nature" irrespective of whatever our evolutionary notions may be. Hull (1974 and 1987), apparently, and Williams (1987) stand opposed to this. I would agree with Hull and Williams, for while we have to assume that there is a world, we can not know it except through our perceptions, which are grounded in our notions of what it is like. Ghiselin's approach leads to a series of assertions (1987b):

> e.g. "Individuals are 'parts' of larger individuals. (John is part of his family.) They are 'members' of classes. (John is male.)" and
> "Some groups, called 'artificial' taxa have to be viewed as classes (such as the warm-blooded animals)."

It should not be solely feminists who see the group 'male' as a coherent, spatiotemporally bounded entity for certain questions, or just a few biologists who treat warm-blooded animals as an individual for certain environmentally related questions. Now if we would want to say that declaring John a _member_ of the male class should not preclude declaring John a _part_ of the male individual, then, of course, the same came be said about species.

Unfortunately, the difficulty is not so easily resolved. Hull does not seem to be so consistent. He argues that the crucial distinction between class and individual is the "relative primacy of similarity and descent" (Hull, 1984). The notion of relativeness might seem to make this view compatible with that attributed to him above -- that it might depend on the question asked. However, this is not the case here. The relativeness is simply something that might make it possible for us _to err_ in calling something an individual or a class. In principle, for Hull, an entity is, and remains always, one or the other. What it is depends on the relative importance of descent and similarity to it.

There are two problems here. Firstly, since relative importance of descent is what makes for an individual, it would seem to preclude ecological and abiotic entities being construed as individuals since such entities belong to hierarchies perceived _mainly_ in terms of development. If individuals are tied to evolution and not also to development (if we forget that descent takes place within a developmental framework), then much of the recent advances in hierarchy theory are vitiated. As well, the determination as to relative descent and similarity is made by human observers and is subject to change as well as being theory ladened in the first instance.

Secondly, the strong case for entities that can only be classes, such as gold or the planets (of the universe) is based on the notion of spatial unrestrictedness and similarity. If the idea of descent is problematic in this regard, then similarity as a distinguishing criteria between individual and class is also problematic. Spatiotemporal unrestictedness may well be an issue, in principle, for many entities, at least some of which would normally be construed as individuals. The total number of cells of my body are unknown by an order of a few percent and the number fluctuates rapidly and by tens of millions. The number of Homo sapiens equally is unknown and fluctuates. Yet the organism and species can both be construed, for certain interests, as individuals. In principle, a piece of gold and planetary bodies are no different, as long as we don't grant primary importance to descent.

This approach makes the relation of natural laws to classes and individuals potentially problematic. Laws apply to classes and not to instances (individuals) -- the systems of physics and chemistry are based upon near-innumerable entities (molecules, photons, etc.) treated statistically. If what makes an entity an individual or a class depends on the questions we ask of it, then we might know that we are dealing with a class when we can usefully speak about the relevance of discovering or applying natural laws for it.

The class of human males, in my view, is based on our "intensional definition" (Salthe, 1985) -- our interests, while males as an individual is based upon a combined evolutionary and developmental path that separates (individualizes) it from all other entities in the universe. However, males are constrained to a certain extent -- we can, in principle, establish laws of nature relevant to males as a group. Here, we treat males as a class and given these evolutionary and developmental constraints, males as an individual is limited in the possible individual it may be. (For Salthe (manuscript) an individual may be viewed as a "class of one member".) The obvious benefit of a feminist perspective and politics is vitiated to the extent that this male context is lost sight of.

2. Connecting Levels

In a hierarchical discussion, care must be taken regarding how we link levels both within and across hierarchies. The working guideline is to find a phenomenon common to both levels as argued for by Allen, O'Neill, and Hoekstra (1984). For example, these researchers have shown that the population and ecosystem levels can be linked through primary production (in that measures of primary production can be made of each level) but not through nutrient cycling, competition, or other phenomena that are not part of both levels (ordinarily, one does not make a measure of nutrient cycling within a population).

The phenomena that are used to investigate a particular level will have an effect on the linkages between various levels -- the impossibility of disentangling, in practice, the structural and descriptive components of hierarchical phenomena presents itself again. For example, if observation of the foraging and eating behavior of organisms is viewed in terms of species interactions, then the appropriate level at which to link the organisms is the community; but, if pollination is the focus of study, then the linked level will be the guild (Allen, O'Neill, and Hoekstra, 1984). In this context Salthe's (1985) argument for the practical need to consider only one level above and one below the focal level is placed in subjective ontological -- i.e., epistemological -- relief. We must, however, choose these adjacent levels carefully for the purposes of our evaluation. When this is done, a method such as loop analysis (Levins, 1974 and 1975) can be an appropriate tool for linking levels (see below and Chapter 6).

3. Isomorphism

Isomorphy has been the object of interest in some hierarchical work (see especially Troncale, 1986), with the methodological consequence that the relationship between the descriptive hierarchies and the structural hierarchies has been forgotten and isomorphy has become reified in a push to discover these laws and regularities everywhere. Empirically based investigations with an interest in a particular level are rendered problematical in this situation. How do we investigate a question such as, why do some levels have few kinds of members (e.g., the alphabet levels of Simon, 1973) while adjoining levels have many kinds of members (e.g. 20 amino acids to many proteins) in an isomorphic context?

Nevertheless, there is a role for isomorphic considerations in hierarchical work. It is fundamental that we appeal to the laws and regularities found in nature in the manner of Winiwarter (1985) and Troncale (1986). I have urged above that we employ an isomorphic criterion for membership _in_ a hierarchy. The member levels of a hierarchy would, as a result, be the same kinds of entities. For example, a cell-phenome-population-community _ecological hierarchy_ is preferable to a cell-genome-population-community _mixed hierarchy_. The latter is not isomorphic with respect to life processes. One is forced to make extra assumptions and arguments about genealogical properties that are irrelevant to an understanding of the other levels and their interrelationships as essentially developmental systems.

However, there are difficult areas. For instance, with respect to selection, the higher level analogue of the ecological population is not the genealogical clade but the ecological community (Damuth, 1985). Damuth's avatars require a focus on the specific community. Similarly, Buss (1987) argues strongly for the changing "primacy" of differing units of selection having a significant effect upon the history of life. In correctly arguing for logical consistency Damuth and Buss, perhaps unwittingly, point out the limits of the isomorphic approach. The power of the concept of natural selection versus selection as sorting is simply vitiated if it is to be held as a significant force at a variety of levels. Natural selection is a concept of great significance because of its clear contextual elaboration focused on the ecological phenome (organism) and population. Neither the clade nor the community seem as cohesive as populations and phenomes with respect to the question of selection. Similarly, neither is species selection wholly analogous to natural selection (Eldredge, 1986). That selection, in principle, operates at different levels should not come to mean that it plays an equally important role at each level.

4. The Functional Hierarchy

We do not have a hierarchically relevant language for the Functional hierarchy. Von Uexkull (1926) developed the concept of 'function circles' in answer to his question: "What does the space look like that surrounds animals?" He was led to distinguish those aspects of the environment which are relevant and irrelevant to animals. (As noted above, Patten, 1982; Bigger and Bigger, 1982; Jackson, 1987; and Odling-Smee, 1988 and manuscript, all grapple with this issue.) The relevant part -- the function circle -- could change in space and over time and is affected by the animal. In this respect, the function circle foreshadows the organism-environment interpenetration of Levins and Lewontin (1980 and 1985).

While it is unclear whether or not he intended to include plants, von Uexkull's function circles were limited to organisms, social species (insect societies), and the human "community". In his own discussion, he does not keep levels distinct from one another and it would be impossible to use his criteria to establish function circles at other levels without consideration of the superorganism concept. However, von Uexkull's rules of genesis and function (roughly consistent with the Genealogical and Ecological hierarchies respectively), combined with the concept of function circles, indicate, for example, that the function circle at the level of the 'Functional hierarchy organism' combines genealogical, ecological, and abiotic properties.

From the perspective of the Functional hierarchy, the function circle would correspond to the realized niche (Hutchinson, 1957) at the appropriate level. Modern niche theory includes work that can be related to each of the four hierarchies discussed above; the level of interest is the population or phenome (Pianka, 1978) or solely the population (Colwell and Fuytuma, 1971). Hutchinsonian niche theory has always been level specific and the phenomena of interest -- r- and K- selection, competition, foraging behavior, etc. -- render the analogy inappropriate for extension to other levels. Niche theory also serves to help us understand an ecological level (population or phenome) but the hierarchical reality of the niche itself has not been a focus of interest, in contrast to the function circle which was included with the entity of interest to von Uexkull.

While we recognize the possibility of inclusive hierarchies, we do not, at present, have distinct terms for many of the correspondi~g levels between hierarchies. Eldredge's (1985) 'Ecological I' (Ecological) and 'Ecological II' (Ecological and Abiotic) hierarchies have common names for all levels below the community-ecosystem. Perhaps we will begin to have precise labels when we perceive the usefulness of clear distinctions as we now do with our Genealogical and Ecological hierarchies.

5. Evolution and Development

Dunbar (1960 and 1972) raised the issue of evolution occurring at the ecosystem level. This stands in clear contrast to Margalef (1968 and continued in the Spanish literature, e.g., Niell, 1981) and Odum (1970), who argued that ecosystems are best seen as developing rather than evolving. Salthe (implicitly, 1985 and explicitly since in a series of presentations) has made a hierarchically based distinction between evolution and development. For Salthe, evolution is the irreversible accumulation of historical information (accidents) and development is irreversible predictable change characterized by stages. Evolution is seen as a genealogical property and development as an ecological and abiotic property. This distinction allows Salthe to locate Zotin's (1972) work on the development of the organism within a hierarchical perspective as well as place the burgeoning Non-Equilibrium Thermodynamics debate in hierarchical perspective. Thus, Ulanowicz (1986), Wicken (1987), and their co-workers are seen to have an externalist-developmental (stage) approach and, in my opinion, to be working within the orientation of the specification hierarchy. Brooks and Wiley (1988) have an internalist-evolutionary approach and thus are within the orientation of the scalar hierarchy. A further aspect of the relationship of Non-Equilibrium Thermodynamics to hierarchical theory would revolve around the distinction of self-organizing systems from other thermodynamically open systems -- self-organizing system are seen in the function circles of the Functional hierarchy and involve elements of the scalar and specification hierarchies.

From the above discussion it is seen that:

- the Genealogical hierarchy is based on evolutionary processes;
- the Ecological hierarchy is based on developmental processes;

. the Abiotic hierarchy is based on developmental processes;

. the Functional hierarchy is based on developmental and evolutionary processes.

The point is that development and evolution are processes usually seen as abstracted from each other with their location as separate phenomena in the relatively abstracted hierarchies. On the surface of the earth, the genealogical, the ecological and, to a major extent, the abiotic entities simply don't exist on their own. They are subsumed and operate within the Functional hierarchy -- the existing functioning hierarchy. We might envision for a given level a spiral where a complete turn (not a circle) represents the stages of the developmental process at that level and evolution would be 'noticeable' irreversible differences in comparable stages from turn to turn.

This development that is not abstracted from evolution represents Salthe's specification development and makes, in a sense, the emergent property of the Funtional hierarchy -- self-organization -- possible. This specification development for a given entity is represented by a single turn of the spiral. Scalar development refers to the playing out of essentially similar paths. We have a spiral instead of a circle endlessly travelled because of evolutionary effects. Abiotic entities tend to collapse into the relatively fully predictable circular trajectory and are often best(?) considered in this manner even when they are caught up in living systems and/or their function circles.

This combined evolutionary/developmental and specification developmental process <u>in living entities</u> is what Salthe calls self-organization. It is these self-organizing entities that possess function circles -- that are capable of interpenetration with their environment. Genealogical, ecological, and abiotic entities are not capable of self-organization on their own -- each is fundamentally mainly evolutionary or developmental in its processes. If we are interested in self-organization, we need to consider a fourth hierarchy where evolution and development are intertwined with the relevant stages -- the Functional hierarchy.

Currently the high status Functional hierarchy entity to investigate is that of Gaia (Lovelock, 1979). Much of the discussion has involved the relevance of terms of reference usually associated with entities closer to the organism (and function circle of the organism) level of reference -- thus, an implicit evaluation of the usefulness of isomorphic considerations in this particular context. On that basis alone one could have predicted a backlash to the Gaia hypothesis and, more unfortunately, ready excuses for ignoring global environmental issues because they are often formulated in "unscientific" terms.

Personally, if I was picking a functional entity to focus upon for purposes of indicating the usefulness of hierarchical investigations, it would be the soil. The level of focus is closer to ourselves even if the average entity size is relatively small (from our vantage point, we being relatively large organisms) for the levels involved. Abiotic entities and death are major aspects of soil processes. Evolutionary and developmental processes are both important while it is hard to imagine much being accomplished in understanding the soil if one of the Genealogical, Ecological, or Abiotic hierarchies is considered a sufficient organizing perspective. Soil is quintessentially a complex, holistic, Functional hierarchy phenomenon.

The Triadic Theory

1. Focal Level Context

Many of the hierarchical discussions in the literature are framed in a two-level context (e.g., most recently, O'Neill, DeAngelis, Waide, and Allen, 1986) despite claims to the contrary (O'Neill, 1989). Almost universally this consists of the level of interest and the level below (but see Campbell, 1974). The level of interest is understood to have characteristics that cannot be explained by extrapolation from the properties of the level below. The two-level structure in the hierarchical tradition is perhaps the clearest indication that hierarchical work is not necessarily the opposite of reductionist efforts. In the two-level approach, the view of necessary context and focus is lost. The two-level theory suggests (or assumes) that the focal level relates to the lower level in the same manner as does the upper level to the focal level and thus allows a new two-level complex for investigation.

focal level   upper level (new focal level)
| similar to |
lower level   focal level (new lower level)

From an empirical viewpoint, however, the primary value of a hierarchical approach is not this two-step transfer of interest but, rather, the need to understand the <u>context</u> of the focal level.

upper level
|
focal level
|
lower level

In a two-level approach, the focal level of interest changes as new kinds of data are collected, while most empirically-focused investigators would prefer to maintain the initially chosen focal level despite the addition of new information. The triadic approach permits us to accomplish the latter.

There has been a triadic tradition in hierarchical theory (e.g., Simon, 1973; Eldredge and Salthe, 1984; Vrba and Eldredge, 1984; and Eldredge, 1985). However, it is Salthe (1984 and 1985) who has developed the approach. In brief, Salthe has, in his triadic system, de-emphasized isomorphic aspects in favor of an explication of the differences between lower level constraints (initiating conditions) and upper level constraints (boundary conditions). Lower level effects are statistical averages of rapid processes, while upper level effects are true constants of slower processes. "The system is fundamentally asymmetrical with respect to crosslevel transactions (Salthe, 1984)." An understanding of the nature of these transactions and their meaning with respect to the focal level could not be achieved within a two-level perspective. Miller (in press, a and b) calls for use of Salthe's triadic perspective in paleoecological studies.

2. Qualitative Loop Analysis and the Triadic View

One question addressed in this study is whether the fossil record can be used to evaluate the empirical worth of hierarchical investigations. This represents the first empirically based hierarchical investigation. Of value is a particular use of Levins's loop analysis (Levins 1975, Puccia and Levins, 1985), which facilitates the investigation of the effects of a parameter change on a system leading to turnover rate changes of a component of the system. For example, a particular environmental (biotic or abiotic) change might affect the relationships that constitute a community in such a way that the age structure of a particular population of that community shifts to a younger average. On this basis, one could predict that the average size of the member <u>phenomes</u> (organisms) of the population would become smaller. This or a similar prediction is possibly testable in a study of the fossil record. However, such a use of loop analysis has had a solely heuristic value in the past. The actual use of loop analysis in an empirical approach poses many problems, especially in a study of the fossil record. The relationship between loop analysis and the triadic hierarchy approach arises from locating the empirically derived, and modelable via loop analysis, entities -- community, population, phenome -- within the upper level, focal level, and lower level respectively of the triadic system. Chapter 6 describes the loop analysis technique and reports on the attempt to apply it in this study.

CHAPTER 4: SAMPLE DESCRIPTION AND ANALYSIS

Introduction

1. Purpose

The purpose of this chapter is to describe and analyze the data of 107 sampling units and 132 species (distinctly identified fossils at the species, genus or higher taxon levels) taken from the Hamilton Group. Since the fossils are distinctly identified (even if not always named) at the species level, except for the catchall nuculid taxa and a few others rare in abundance, the term species rather than taxon will be used. From this I will take the appropriate subset of data to be used for the community level and hierarchically embedded investigations discussed in Chapters 5 and 6.

Here, I wish to reduce and rearrange the data so as to investigate its usefulness for questions relating to fossil communities. The effort is an "exploratory" one (Tukey, 1977). I will also place the data in the given structure of the upper Hamilton, Windom, and Ledyard time frames as well as in the derived structure of community types. Given these purposes and the large data set, multivariate analyses will be the centerpiece of the analytical techniques employed (Neff and Marcus, 1980).

It is useful to note that analysis is being made only for the data at hand. Thus, while meaningful statements can be made for the data used in this study, no attempt will be made to generalize to a larger situation. That effort would require an inferential (Pielou, 1984) or "confirmatory" (Tukey, 1977) approach to the multivariate data. Following this, when I refer to the Hamilton, Ledyard, Windom or various community types with respect to the analyses of the sample, I am in fact referring to the set or subset(s) of the sampling units and fossils used in this study.

Finally, when Gauch (1982) talks about multivariate analyses "revealing the structure" or Pielou (1984) discusses finding the "latent structure", they do not mean finding the underlying structure of a community or community type. What they do mean is finding the structure of the sample. This sample structure consists of observed patterns. The patterns are observable because the data has been simplified and rearranged systematically. Based on these observed patterns I will tentatively group the sampling units into various community types. What confidence I have at this point in the specification of community types comes from the belief that human observed pattern should have some relationship to natural processes. In the following chapter, I will apply a series of community level and population level measures. If the results of that and the hierarchically oriented effort of Chapter 6 support the grouping of sampling units into the community types investigated, I will have greater confidence that I have identified a community type. The multivariate analyses undertaken alone would not be sufficient, although discussion in the literature often assumes so.

2. Sampling Units

Table 1.2 notes the localities and Members of the sampling units. Placing the Chenango Valley sampling units (and localities) in the proper Formation and Member and in proper relation among themselves became the initial task for this part of the study. Previously (Rollins, Eldredge and Linsley; 1972), the Bradley Brook quarry had been placed in the Ludlowville (Linsley) and the Deep Spring quarry had been placed in the Moscow-Windom (Eldredge). Field work by Colgate University geologists (especially Selleck) has established that the same bedding plane could be located in the Bradley Brook, Geer Road and Lebanon Center Road quarries. In Bradley Brook and Lebanon Center Road a thin calcareous fossil layer is found approximately 2 meters above this bedding plane. In Bradley Brook, Geer Road and Lebanon Center Road a phosphate nodule bed is found approximately 5.5 meters below the bedding plane.

It was when this common bedding plane had been pointed out to me by Linsley that I decided to include parallel sampling units from the three quarries for my thesis work. I felt that I could take a series of sampling units from different localities which are inferred to represent nearly the same point in time when deposited. This would be a benefit for community level questions.

I decided to pursue my sampling in the Deep Spring quarry as there was some interest among paleontologists in seeing if the common bedding plane might be found there as well. There has been an uncertainty about locating this quarry in a different Formation from the other three. However, no phosphate nodule bed or calcareous fossil layer was to be seen.

Based on the sampling undertaken, it now appears to me that the bedding plane in each of these four quarries that served as my youngest Chenango Valley sampling unit is a common bedding plane. This is based on the following observations:

- in Geer Road, Lebanon Center Road and Deep Spring I observed a prominant Sulcoretepora (and other bryozoans) layer (4 cm to 6 cm thick) starting from 15 to 20 cm below the bedding plane
- in each of these three quarries, my sampling stopped at a thin coquina layer starting from 50 to 55 cm below the bedding plane

On this basis, I would argue that these indicate a common bedding plane, bryozoan layer, and coquina layer for the three quarries. Because quarrying activities had disrupted the rocks immediately below the bedding plane, I was prevented from establishing the existence of the common bryozoan and coquina layers in the Bradley Brook quarry. However, based on the phosphate nodule and calcareous fossil evidence noted above, there is little doubt that the common bedding plane extends into Bradley Brook as well.

There seems to be informal agreement (e.g., Brett, personal communication) that these quarries should be placed in the Windom if they are to be placed together and that is how I treat them in this study. Figure 4.1 shows the relationships seen in the four quarries. Thus, one question answered in this study is the relationship of Deep Spring to the other three quarries and, more specifically, the existence of a common bedding plane and other layers in the four quarries.

Initial Focus of the Analyses: How Raw Data Is Scaled

Paleontological studies aimed at eliciting information on the depositional environments of a sample often make use of multivariate analysis (e.g., several studies reported in Brett, 1986a). Studies based on community questions also make use of multivariate analysis (e.g., several studies reported in Gray, Boucot and Berry, 1981). One issue that is of interest to me is whether the results of a study (or at least the multivariate part of it) are affected by the way the raw data is grouped or scaled prior to analysis.

In the Brett volume, for instance, Grasso (1986) scaled his data into seven relative abundance groups while Savarese, Gray and Brett (1986) and Miller (1986) used presence-absence for their scaling. Would different scaling affect the results?

In an attempt to address this question, I used several different scaling methods for the fossils in my sampling units. These methods are:

1) raw data adjusted for equal rock volume ERV
2) per cent %
3) presence-absence P/A
4) Gauch octaves GO
5) relative abundance groups RAG

For the multivariate analyses, only species from brachiopod, pelecypod, bryozoan, gastropod, and trilobite taxa were included (112 of 132 species). Species from other taxa were not as presisely counted at all times.

1) ERV When comparing sampling units based upon different rock volumes (e.g., for a full 107 sampling unit comparison), adjustments to the raw data due to different rock volumes were necessary. Brett and Pilette counts were multiplied by a factor of 3 when they were evaluated along with the McCollum (1980) counts. Appendix 4.1 provides the basis for these adjustments.

2) % The raw unadjusted data was converted into percent of the sampling unit total accounted for by each species.

3) P/A All species present in a sampling unit were scored equally as 1 with species not present scored as 0.

4) GO Gauch (1982) has proposed the following octave scale for species in a sampling unit:

presence %	score
0	0
$0<x<0.5$	1
$0.5\leq x<1$	2
$1\leq x<2$	3
$2\leq x<4$	4
$4\leq x<8$	5
$8\leq x<16$	6
$16\leq x<32$	7
$32\leq x<64$	8
$64\leq x\leq 100$	9

5) <u>RAG</u> Six relative abundance groups were scored:

presence %	score
0	0 absent
$0<x<1$	1 present
$1\leq x<3$	2 rare
$3\leq x<10$	3 common
$10\leq x<50$	4 abundant
$50\leq x\leq 100$	5 dominant

In addition, analyses were undertaken with all species identified, with rare species removed (rares out), and with the most abundant species and rare species removed. This last represents one way of seeing if community patterns are distinguishable from dominant species patterns (Franz, personal communication).

The multivariate methods used in this study were clustering, three forms of principal components analysis, and an examination of the correlation matrix. Two basic assumptions involved in the use of these methods are that the relationships are linear and the important populations are present (Neff and Marcus, 1980). These methods were undertaken using SAS on the CUNY mainframe.

The SAS clustering method (here called <u>CLUS</u>) was hierarchical, using a normalized centroid (all points are used in the cluster) measure in order to define intercluster distance. Variables were standardized to a mean of 0 and a standard deviation of 1. Normalizing the data was chosen to emphasize similarity based upon relative proportions (Pielou, 1984).

The principal component analysis was undertaken for covariance (PCCOV) and correlation (PCCOR) matrices each using mean corrected data. Scores have variance equal to the corresponding eigenvalues. In addition, a third principal component analysis was undertaken using a covariance matrix without mean corrected data (PCCOVN). Standardized scores tend to emphasize the contributions of the less common populations (Pielou, 1984). This seems less appropriate (given taphonomic issues) for a paleocommunity analysis.

The correlation analysis (CORR) was accomplished using the Pearson product-moment technique.

No attempt was made to evaluate different clustering techniques, e.g. nearest-neighbor, farthest-neighbor, etc. Rather, the major effort for technique evaluation was aimed at the different methods of scaling data.

Initial Analysis

One of the first problems to be faced was that of choosing an initial bench mark. It is impossible to systematically evaluate over 100 different print-outs and over 200 plots without some preconception of what to compare with what.

The strength of this study lies in the relatively large data set: 107 sampling units and 132 species. I decided to begin by comparing the CLUS, PCCOV, PCCOR, PCCOVN, and CORR results for equal rock volume (ERV) for the complete Hamilton sample including rare species. These five print-outs were the initial starting point.

In addition, I started with an expectation based on visual analysis of the data. Sampling units 7, 17, 23, 34, 44, and to a certain extent 30 (see Table 1.3) are quite distinguishable from all other sampling units. These nuculid layers have fewer species and have a unique and overwhelming dominant rarely even present in other sampling units. I expected that a useful analytic technique should be able to distinguish these 5 (and possibly 6) sampling units from the remaining 101 sampling units.

While these initial criteria served to begin evaluation, I wished to add a criterion that would allow me to take advantage of the complete data set and also allow the use of the various multivariate and scaling techniques. This criterion is robustness (Levins, 1966) -- consistency of results across different techniques and methods of scaling data. In the end, I based my choice of community types on consistency of results.

Grouping Sampling Units

Table 4.1 gives the grouping for the various methods used. There should be no assumption that readily distinguishable groupings and placement of most sampling units within groups is necessarily a better use of the data. It is quite possible that the most useful analysis of the sample represents a rather fuzzy grouping of relatively few sampling units. What is clear is that different methods can give quite different results. It is of interest to know how they support each other, compliment each other, and help point out various issues and problems.

Following is a brief description of the grouping seen in Table 4.1. A minimum of 3 sampling units was considered necessary for there to be a group.

1) Cluster, Equal Rock Volume.

The CLUS-ERV tree was principally built by adding one observation at a time to the existing main cluster. This happened in 60 of 106 cases. The result is few definable clusters. The normalized centroid distance was always very small and exceeded 0.07 in only 1 of 106 instances. The nuculid group is incompletely defined and the largest group consisting of eighteen sampling units is very weakly defined.

2) Principal Components Correlation, Equal Rock Volume.

The PCCOR-ERV eigenvalue scores were very low. The first eight eigenvalues accounted for only 39.7% of the total. In general, there were few readily observable groupings from either the plots or scores. Those groups were often strung out in the plots. The nuculid group was not identified in any of the first eight scores. (When I came back looking for particular groupings identified readily by other methods, several of the groups were identified.)

From the PC1xPC2 plot (figure 4.2) two groups were identified. The first contained 23 of the 28 sampling units eventually defined as the *Chonetes-Ambocoelia* community type. These all scored high on PC1. The second contained 9 of the 11 sampling units (plus one other) eventually defined as the *Ambocoelia-Craniops-trepostomate* community type. This group, although a bit strung out, scored low on PC1 and quite high on PC2. The "outliers" to both of these groups consisted of sampling units eventually included in the respective community types. In addition, the PC2 scores split the eventually defined *"Leiorhynchus"-Devonochonetes* and *Devonochonetes-Ambocoelia* community types from the remaining sampling units.

From the PC1xPC3 plot 4 of the 5 sampling units (plus one other) that comprised the *Tropidoleptus-Truncalosia* community type were identified.

High scores for the first three eigenvectors were always positive and the species scoring high were generally the most abundant members of the groups identified by high scores on the respective PC.

3) Principal Component Covariance - No Mean Correction, Equal Rock Volume.

PCCOVN-ERV had relatively strong eigenvalue scores with the first eight accounting for 95%. There were more groups, more sampling units grouped, and these groups were easier to pick out than with either CLUS-ERV and PCCOR-ERV. Groupings still tended to be strung out but "patterns" were more distinguishable. The nuculid community type is readily identified in the PC6xPC7 plot due to the high scores of the member sampling units on both PC's.

From the PC1xPC2 plot two groups are identified. The first is 21 of the 28 sampling units of the eventually defined Chonetes-Ambocoelia community type and the second is 6 of the 24 sampling units of the eventually defined "Leiorhynchus"-Devonchonetes community type.

From the PC1xPC3 plot (figure 4.3) another group of 10 sampling units is identified based on high scores on PC3. The member sampling units of this group were eventually assigned to 3 different community types. (In retrospect, PC3 was seen to split Devonchonetes-Ambocoelia from "Leiorhynchus"-Devonochonetes based upon + and - scores respectively for the member sampling units.)

From the PC1xPC5 plot a group of 7 of the 17 (plus one other) members of the eventually defined Devonochonetes-Ambocoelia community type was identified.

Finally, from the PC2xPC3 plot two groups were identified based on clusters in the center of the plot. The first comprises 12 of the 24 sampling units of the "Leiorhynchus"-Devonchonetes community type and the second 10 of the 17 sampling units of the Devonochonetes-Ambocoelia community type.

Several of the high scores on various eigenvectors were negative. These were scores for dominant species of community types whose member sampling units were not identified as a group for the respective PC score. Another distinction from the PCCOR-ERV eigenvectors was the very high positive scores of the dominant species for member sampling units of groups identified by the respective PC score. For instance, Chonetes cf. lineatus has a value of +0.95 on the first eigenvector with only one other species (Ambocoelia umbonata) scoring above 0.09.

4.1) Principal Components Covariance, Equal Rock Volume

PCCOV-ERV had relatively strong eigenvalue scores with the first nine accounting for 95%. While having fewer groups identified than with PCCOVN-ERV, those identified were never less and, in one instance, was clearly more similar to eventually defined community types. The nuculid community type is clearly identified on the PC3xPC7 plot.

From the various plots, the following groups were identified:

- 21 of 28 sampling units of Chonetes-Ambocoelia
- 7 of 24 sampling units of "Leiorhynchus"-Devonochonetes
- the 6 sampling units of nuculid
- 13 of 17 (and one other) sampling units of Devonochonetes-Ambocoelia
- a group of 7 sampling units drawn from the remaining three community types eventually defined

As with PCCOVN-ERV, there were several high eigenvector scores that were negative. Again these were scores for dominant species of community types whose member sampling units were not identified as a group for the respective PC score. However, the negative score for nuculids on PC3 and the high positive score on PC7 enabled the _nuculid_ community type to be identified on the PC3xPC7 plot.

4.2) Principal Components Covariance, ERV-Rares Out.

PCCOV-NR eigenvalue and eigenvector scores were nearly the same as for PCCOV-ERV. Three of the five groups identified were identical to those identified with PCCOV-ERV: the full _nuculid_ group, and the partial _"Leiorhynchus"-Devonchonetes_ and _Chonetes-Ambocoelia_ groups. However, the mixed grouping was not identified and the eventually defined _Devonochonetes-Ambocoelia_ community type was seen as two separate groups.

4.3) Principal Components Covariance, Percentage.

PCCOV-% eigenvalue and eigenvector scores were lower than those for PCCOVN-ERV, PCCOV-ERV, and PCCOV-NR. They were quite similar to the scores for PCCOR-ERV. However, not only were the groupings generally less strung out than with previous efforts, the groupings themselves were closer to the eventually identified community types. The PC1xPC2 plot was the clearest plot of any seen in the study in showing several groups at one time (Figure 4.4). From this plot, the following groupings are seen:

- 21 of 24 sampling units of "Leiorhynchus"-Devonochonetes

- 16 of 17 sampling units of Devonochonetes-Ambocoelia

- the 5 sampling units (and 3 others) of Tropidoleptus-Truncalosia

- 5 of 6 sampling units of nuculid

- the 28 sampling units of Chonetes-Ambocoelia

- a group of 22 sampling units combining Ambocoelia-Craniops-trepostomate and Ambocoelia-Tropidoleptus

Other PCCOV-% plots showed one or more of these groups more clearly, but this plot shows the most groups. Yet, the first two principal components account for only 55.7% of the eigenvalue score.

4.4) Principal Component Covariance, Presence-Absence and Gauch Octaves and Relative Abundance Groups.

These three methods had very low eigenvalue scores (many more than 10 required to reach 95%) and numerous species with relatively high eigenvectors (not surprising given the grouping method). Fewer groups were identified but these tended to be consistent with eventually identified community types. What were not identified, even in part, were groups from "Leiorhynchus"-Devonochonetes and Devonochonetes-Ambocoelia. Unique to the other principal component methods, the Ambocoelia-Craniops-trepostomate and Ambocoelia-Tropidoleptus groups are clearly identified.

5.1) Correlation, ERV and ERV-No Rares and Percentage.

These three methods produce identical groupings and nearly identical scores. No member of any group has a p-value of more than 0.0001 for its link with any other member of that group. For the following groups, the r-values given are for ERV but these are insignificantly different than the comparable r-values for the ERV-NR and %:

- the 28 sampling units of Chonetes-Ambocoelia (Table 4.2). The average lowest r-value between any two members is 0.74 while the average highest r-value between any one member and the closest non-member is 0.22. Seventy percent of the 378 correlations are .90 or higher.

- the 6 sampling units of nuculid. The average break r-value between within and without members is 0.91 and 0.17.

- 4 of the 5 sampling units of Tropidoleptus-Truncalosia. The average break r-value between within and without members is 0.92 and 0.55.

- the 10 sampling units of Ambocoelia-Tropidoleptus. The average break r-value between within and without members is 0.83 and 0.76. A few sampling units have higher r-values with some of the members of Ambocoelia-Craniops-trepostomate than they do with a few of the other sampling units of their group.

- the 11 sampling units of Ambocoelia-Craniops-trepostomate. The average break r-value between within and without members is 0.69 and 0.59. A few sampling units (61, 62, and 65) have higher r-values with some of the members of

Ambocoelia-Tropidoleptus than they do with a few of the other sampling units of their group. Sampling units 66, 67, and 69 generally have the lower r-values within the group.

- 15 of the 17 sampling units of Devonochonetes-Ambocoelia. The average break r-value between within and without members is 0.82 and 0.76. Several sampling units (especially, 35, 38, and 39) are consistently mixed in with several members of "Leiorhynchus"-Devonochonetes. Sampling unit 32 is usually the lowest member r-value but is consistently higher than non-member r-values.

- the 24 sampling units of "Leiorhynchus"-Devonochonetes. The average break r-value between within and without members is 0.81 and 0.75. Several sampling units (14 and 26 especially and 29) are consistently mixed in with several members of Devonochonetes-Ambocoelia.

5.2) Correlation, Gauch Octaves and Relative Abundance Groups.

These two grouping methods give nearly exactly the same results. The results are quite similar to the previously discussed Correlation methods. The same seven groupings are identified. In a few groups, one or two sampling units fewer are identified as being part of the group. The r-values are always lower and in a few instances there are no real breaks between within and without members. However, the ordering is very much the same.

5.3) Correlation, Presence-Absence.

CORR-P/A gave fewer groups and did not identify the nuculid group. The groups identified generally had fewer sampling units than those found using other Correlation methods. The r-values are relatively low (although the p-values always continue to be lower than 0.0001) and in several instances there are no real breaks. The ordering is somewhat the same as with the other Correlation methods.

Community Types Identified Through Multivariate Analysis

1. Community Types Identified

The 107 sampling units can be grouped as follows:

1) "Leiorhynchus"-Devonochonetes

Sampling units 4-6, 9-16, 18-22, 24-28. Sampling units 2, 8, 29 are close to this group. Sampling units 15, 16, 18-21, 29 form a strong subgroup. (Several members of this community type are close to several members of the Devonochonetes-Ambocoelia community type.)

2) Devonochonetes-Ambocoelia

Sampling units 31, 33, 36-39, 41, 43, 45, 46. Sampling units 32, 35, 40, 42, 51, 53, 58 are close to this group. (Sampling units 35, 37, 38, 40, 42 are close to several members of the "Leiorhynchus"-Devonochonetes community type.)

3) _Tropidoleptus-Truncalosia_

Sampling units 52, 54-56. Sampling unit 50 is close to this group.

4) _nuculid_

Sampling units 7,17,23, 30, 34, 44.

5) _Ambocoelia-Craniops-trepostomate_

Sampling units 59-69. (Several sampling units are close to several in the _Ambocoelia-Tropidoleptus_ community type.)

6) _Chonetes-Ambocoelia_

Sampling units 70-89, 91-93, 95-97. Sampling units 90, 94 are close to this group.

7) _Ambocoelia-Tropidoleptus_

Sampling units 100-107. Sampling units 49, 57 are close to this group. (Several sampling units are close to several in the _Ambocoelia-Craniops-trepostomate_ community type.)

Ungrouped: 1/3/47/48/97/98.

With respect to the sampling units used in this study:

The _"Leiorhynchus"-Devonochonetes_ community type is found in the Ludlowville Ledyard (Alden -- McCollum, 1980) of western New York and the _Devonochonetes-Ambocoelia_ is found in the Ludlowville Ledyard (Elma -- McCollum, 1980) of western New York. Each contains several sampling units closely related to the other such that there is not a sharp break between community types.

The _Tropidoleptus-Truncalosia_ is a clearly distinguishable community type that occurs near the top of the Ludlowville Elma in western New York. The _nuculid_, also a clearly distinguishable community type, reappears throughout the Ludlowville in western New York.

The Ambocoelia-Craniops-trepostomate is a Ludlowville Alden community type found in western New York with some relationship to the Ambocoelia-Tropidoleptus community type found in the Moscow Windom and in the upper Ludlowville Elma of western New York.

Finally, the Chonetes-Ambocoelia is a clearly distinguishable community type that is found in the Moscow Windom of central New York.

It is apparent from the literature, especially the work of Brett and Baird and their co-workers, that these Members, Formations, and localities are not the only place that one would find most or all of the community types, or closely similar ones, noted above (e.g., Chonetes dominated assemblages are found throughout the upper Hamilton). Thus, the groupings and placements refer only to the study sample. Further discussion will be found below.

2. Comparison of Different Scaling Methods and Different Multivariate Techniques

Having identified the community types, it is possible to evaluate the different methods of scaling the data and the different multivariate techniques employed. The procedure is somewhat circular since the community types were originally identified based on the comparisons of the results of the evaluation of different scaling methods under different multivariate techniques.

This is a type of chicken-egg issue but does not constitute a problem since the circularity is transcended by a higher level of organization -- the application of the criterion of robustness. It is somewhat, but only somewhat, arbitrary where one starts in this analysis, but after the initial iteration through the various methods and techniques, one does not stand in the same location as at the start. The criterion of robustness gives a good deal of confidence in the identification of community types, much more so than, for example, with the sole use of an Equal Rock Volume Correlation analysis even though this particular procedure happened to produce (in this particular study) nearly the same grouping of community types as does the robustness approach.

Table 4.3 shows the number of "correctly" identified sampling units grouped into the proper community type by the various scaling methods and multivariate techniques employed in this study. Table 4.4 simplifies the information of Table 4.3 into relative performance categories.

With respect to multivariate techniques (each based upon Equal Rock Volume), Correlation outperformed the three types of Principal Component procedures used while the single instance of Cluster gave the poorest results. <u>However, as noted above, nothing should be read into these</u>

results regarding the relative value of the various multivariate techniques. There are several other techniques of clustering and principal component analysis available in addition to those used in this study. I used a variety of techniques more for robustness considerations than for any other reason. What is apparent is that one should not limit oneself to just one multivariate technique in a study of this type.

As for evaluating the different methods of scaling the data, there is considerable effect based upon the type of multivariate analysis used. In a Correlation analysis, Equal Rock Volume, ERV with rare species out, and Percentage all give very good results -- that is, they closely correspond to the community types identified based on evaluation of all of the procedures. There is then a considerable drop off in performance if Gauch's Octaves or Relative Abundance Groups are used, and an additional strong drop off in performance if simple Presence/Absence is used.

However, if the PCCOV technique is used there is a relatively good performance with Percentage scaling and a relatively poor performance with the use of any of the other five scaling methods.

One should beware the too easy application of the Presence/Absence (P/A) method of scaling data. If I had relied solely upon P/A in this study, the results would have been considerably different for identifying community types. More importantly, the community and hierarchically oriented explorations of Chapters 5 and 6 would not have been suggested. Since I believe useful information and further understanding of communities and hierarchies has resulted from the efforts reported in these two chapters, this would have represented a real loss.

When considering the scaling and multivariate techniques used in this study, the use of Octaves and Relative Abundance Groups also lead to poor identification of community types. However, even with these methods, essentially the same sampling units identified for use in Chapters 5 and 6 for further community and hierarchical explorations were identified with the Correlation technique and approximately one-half of the sampling units were identified with PCCOV.

The use of Correlation with Equal Rock Volume, both with and without rares, or with Percentage and the use of PCCOV with Percentage produces the same subset of sampling units subsequently used in Chapters 5 and 6. However, using PCCOV with either type of ERV gave approximately one-half of the subsequently used sampling units.

It is interesting that use of the Percentage scaling method gives at least as good results as using ERV and the latter does about as well with either rares included or excluded. Thus, in studies of this type, where data is used from different investigators and initially based on considerably different sampling unit rock volumes, it is useful to expect that little information will be lost by using Percentages rather than actual fossil counts. This conclusion is supported by the application of the various methods and techniques to subsets of the sample based on a single field investigator's sampling units.

Again useful for paleontologists, is the essentially equal relevance of being able to exclude rare species at least for the multivariate part of any analysis. It is equally important to know that one must be very careful in further scaling data, especially in using simple Presence/Absence. Where possible, nothing further abstracted from the actual field counts than Percentages should be used -- at least for community analysis.

Other Assemblage Based Analyses

1. Dominant and Rare Species Removed

To what extent are the community types perceived with the multivariate analysis derived mainly from the effects of the most abundant species? Average abundance of the dominant species per sampling unit is over 52% and with the six nuculid sampling units removed (where the average abundance of the dominant is over 85% for the catchall designation nuculid), the average is still over 50%.

Do the remaining species contribute to the patterns observed? To look at this question, I undertook a PCCOV and CORR analysis of the sampling units with the dominant species and rare species removed.

The PCCOV bore little resemblance to patterns perceived previously. Eigenvalue scores were low with the first totalling 32.6% of the total and eleven required to reach 95%. A relatively unique eigenvector pattern was seen. There was generally one overwhelming dominant with a high positive eigenvector and all other scores were less than 0.10. The dominant value was attached to the species that was originally the second dominant in the various groups.

The plots were generally uninformative, tending to be strung out with a slightly dense end at the lower score end. Only the PC1xPC2 plot produced a bit of an "L" shape with a group of sampling units somewhat isolated. These were sampling units 14-16, 18-20, 29 and 50. These, except for the last, are members of the "Leiorhynchus"-Devonochonetes community type. The nearest sampling units to these also tended to be from this community type. None of the other community types were found, even in part, with PCCOV.

On the other hand, CORR results were somewhat supportive of the previous patterns. The clear break between types almost always seen with the CORR applied to data including dominants was essentially lost. However, the original ordering remained to a large extent:

1) "Leiorhynchus"-Devonochonetes. 20 of 24 sampling units hold together. Fourteen of the first fifteen scores are from the group of 20 on the average with the interloper in all cases but one being sampling unit 44. Sampling units

2, 8, 26 and 27 fall out of the type while 3, 17, 50 and 56 are relatively close.

2) Devonochonetes-Ambocoelia. 12 of 17 sampling units hold together. The first seven scores are from this group of 12 on the average. Sampling units 32, 39, 51, 53 and 58 fall out of the type with the latter 3 remaining close together among themselves.

3) Tropidoleptus-Truncalosia. This group of 5 falls apart.

4) nuculid. This group of 6 falls apart.

5) Ambocoelia-Craniops-trepostomate. This group of 11 essentially falls apart and the r-values are quite low.

6) Chonetes-Ambocoelia. 21 of 28 sampling units hold together. The first eleven scores are from this group of 21 on the average. Sampling units 74, 76, 82, 84, 90, 96 and 97 generally fall out.

7) Ambocoelia-Tropidoleptus. 7 of the 10 sampling units hold together. They along with sampling unit 55 are the first eight always with each other. Sampling units 49, 103 and 107 generally fall out.

Without belaboring the point, it appears to me that a remarkable amount of similar pattern remains when the dominant species is removed from a multivariate analysis when compared to the full data set including the dominant. The point is neither that previously identified community types are precisely identified nor that one should even attempt a community analysis starting from this approach.

It is simply that a significant amount of previously identified pattern remains under this very grave adjustment of the data. On the average, 50% of the fauna (in the form of one species) is removed and not all of the pattern is lost by any means.

2. Simple Ranks of the Three Most Abundant Species

Table 4.5 gives the simple ranks of the three most abundant species for each sampling unit. Table 4.6 organizes this information by community type. As can be seen from these tables, it is possible to essentially recover the community types identified in the multivariate analysis. The *Ambocoelia-Craniops-trepostomate* community type would be split into two separate groups. Sampling units 1 and 98 would be placed within community types whereas they were previously left ungrouped.

Thus, for this particular study, a large amount of the grouping information derived from the multivariate analysis is obtained by simply looking at the three most abundant species in each of the sampling units. From this, one may choose, with fair confidence, community types and identify the major contributors to these types.

The rationale for a multivariate approach lies with other factors:

1) reinforcement of the simple ranking procedure;

2) greater precision -- patterns were seen with the multivariate analyses that were not seen with the simple rankings; and,

3) the possibility of taking up a variety of other questions in addition to the grouping and contribution to this grouping of the most abundant species.

3. Dominance Diversity Curves

Hughes (1986) has proposed a "dynamics model" with respect to accounting for relative abundance distributions (see Chapter 2). It predicts larger numbers of organisms for the abundant species than does the log-series model and a greater number of rare species than does the log-normal model thus giving a "deeply concave" dominance diversity curve. Hughes' work derives from an extensive review of Recent benthic marine data and is technically applicable only to sampling units consisting of 30 or more species.

Here, I am working with the fossil record and no sampling unit has more than 29 species. Thus, there is to be no test of Hughes' model. But I am interested in what dominance diversity patterns are seen in these fossil sampling units. Accordingly, I generated dominance diversity curves for the eighteen sampling units having 20 or more species. Figure 4.5 shows the resulting curves.

The nine sampling units from the Chonetes-Ambocoelia community type generally fit the dynamics model being more or less concave. The two sampling units from the

Tropidoleptus-Truncalosia community type give relatively classic log-normal curves. The seven sampling units from the *Ambocoelia-Craniops-trepostomate* community type vary between log-normal and dynamics distribution and the individual curves are generally not as clear as to which model they fit as the curves from the previous two groupings.

Due to the small number of sampling units reviewed and the relatively low number of species in each sampling unit it is not appropriate to make definitive statements. However, it is obviously interesting that two community types show different and consistent dominance diversity curves. It would be worthwhile in the future to undertake further sampling to see if there is a continued persistence of log-normal curves associated with the *Tropidoleptus-Truncalosia* community type and the dynamics curve associated with the *Chonetes-Ambocoelia* community type. If such patterns persist here and in other community types examined, it would then be useful to seek possible physical and biological clues for the observed pattern including the pattern for those community types where no consistent curve is found. This last pattern, of course, only becomes of interest when it exists as an anomaly.

Community Types: Species and Community Characteristics

In this section, all species, including those not used in the multivariate analysis, are incorporated into the evaluation and discussion as appropriate.

1. Dispersion, Fidelity, and Diversity

Table 4.7 lists the species found in each of the community types distinguished in this study. Also included in the table are the frequency of occurrence in the sampling units that are grouped under each community type and the relative abundance of the species in each community type.

While the relative abundance of most species is related to their relative appearance in the sampling units, for each community type there are several species for which this dispersal pattern does not hold. Table 4.8 lists, for each community type, those species that show either a relatively high sampling unit appearance to abundance ratio or a relatively low sampling unit to abundance ratio. Each community type (except, possibly, *Tropidoleptus-Truncalosia*) favors one ratio or the other. These relatively unevenly dispersed species comprise from 12% to 27% of the species of a given community type.

Table 4.9 lists those species that have *characteristic* or *ubiquitous* fidelity patterns with respect to the community types evaluated in this study. The remaining species can be considered to be *intergrading*. These terms are borrowed from Johnson (1972) who used them for his theory of succession patterns for which paleoecologists might search in the fossil record. I have already criticized his attempts and those of others at developing a paleoecological theory of succession (see Chapter 2). To use these terms in this study, the notion of local area and same time assumed by Johnson is not appropriate. For this study:

- characteristic refers to species found in only one community type

- intergrading refers to species found in two to five community types

- ubiquitous refers to species found in six community types (if the missing community type is nuculid) or all seven community types

The nuculid adjustment was made because of the obviously different taphonomic history of the sampling units comprising this community type. This is shown by the different preservational quality of the fossils (McCollum, 1980) and that the nuculid community type has less than one-half the identified species seen in any other community type.

The ratio of characteristic to total species for each community type would seem to indicate that the Chonetes-Ambocoelia community type is unique in having a much higher ratio than that found for any other community type. However, there are two considerations here:

1) There are considerably more species in the Chonetes-Ambocoelia community type than in any other community type. This would not account for all of the difference because if the "extra" species were removed and each just happened to be a characteristic one, the Chonetes-Ambocoelia community type would still have more characteristic species than any other community type. (Excepting the nuculid community type which has so few species to begin with.) These "extra" species probably occur, in some part, due to the sampling method employed for these particular sampling units (see Appendix 4.1). Still, it is hard to imagine that all of the "extra" species would be characteristic ones.

2) There is also a slight positive relationship between characteristic species and number of sampling units in a particular community type. However, the ratio of characteristic species to sampling units for each community type shows Chonetes-Ambocoelia to be twice as high as any other community type and most often six to seven times as high.

Only with the Ambocoelia-Craniops-trepostomate community type might the above considerations account for a large portion of the difference between it and Chonetes-Ambocoelia regarding characteristic species patterns. Chonetes-Ambocoelia (and, perhaps, Ambocoelia-Craniops-trepostomate) has a significantly greater percentage of characteristic species than the other community types.

This is probably accounted for by the fact that the Chonetes-Ambocoelia community type is the sole central New York upper Hamilton community type while the other six are found in western New York. Considerations of Formation or Member will not account for the difference. Before the effect of geographic locality can be ascertained, other community types would have to be sampled for in the Chenango Valley and other central New York State localities, and it would have to be seen whether this would lower the number of characteristic species of the Chonetes-Ambocoelia community type. Only then would it be worthwhile to pursue biological and environmental explanations for the "phenomena".

As for the ubiquitous species, the two most important are Ambocoelia umbonata and Mucrospirifer mucronatus. These are relatively abundant and Ambocoelia is, in fact, the dominant or second dominant species in four of the seven community types established in this study. One effect of this is that these species (especially Ambocoelia) sometimes showed high eigenvector scores for Principal Component plots in which community types were relatively less distinguishable. This is not noise -- the fuzziness is quite real when ubiquitous species are relatively dominant ones as well.

2. Trophic-Mobility-Substrate Relations

Figure 4.6 gives the trophic-mobility-substrate relationship for each species included in this study.

Following this, Figure 4.7 gives the niches (based on the characteristics under discussion here) occupied in each community type by the sampled fossils. Table 4.10 gives the percentages for those niches with precisely counted species.

As can be seen from Figure 4.6 and Table 1.4 (upon which Figure 4.6 is based), there are ten species for which niches are not very well established. There are several others that I have characterized differently than did Bowen, Rhoads, and McAlester (1974) in their seminal work on trophic-mobility-substrate relations. These distinctions are based upon discussions with Brett and Baird.

Based on Table 4.10, the seven community types described in this study can be placed in four kinds of communities based on niche patterns:

1) nuculid -- Infaunal Mobile Deposit Feeders comprise 90% of the total for the seven niches for which there are precise species counts. McCollum (1980) argues that part of this high percentage is probably based on trophic group amensalism arising from the substantial bioturbation of sediments by the active nuculids. Similar amensal effects were described in the Recent benthos by Rhoads and Young (1970) -- see discussion in Chapter 2 above.

2) Ambocoelia-Tropidoleptus, Ambocoelia-Craniops-trepostomate, and "Leiorhynchus"-Devonochonetes -- Epifaunal Low Attached Suspension Feeders total more than 45% of the identified fauna. If Ambocoelia is considered an Epifaunal Immobile Free Suspension Feeder as argued for by Bowen,

Rhoads, and McAlester (1974), then the Ambocoelia-Tropidoleptus and Ambocoelia-Craniops-trepostomate community types would be placed in the following niche pattern.

3) Tropidoleptus-Truncalosia, Devonochonetes-Ambocoelia, and Chonetes-Ambocoelia -- Epifaunal Immobile Free Suspension Feeders comprise at least 65% of the identified faunas in this pattern.

As can be seen, a particular niche pattern can be established with different species -- including different dominant species.

Community Types in the Hamilton

1. Comparison with other Characterizations

McCollum (1980) places her sampling units in "general assemblage" types. For the most part they correspond to the community types described here based upon application of multivariate analysis to McCollum's sample (Table 4.11). In generalizing, some problems arise with McCollum's types. For instance, sampling units 6, 13, 25, 29, 31, and 35 are included in types named after species not present in these particular sampling units.

The main differences are in characterizing sampling units 1 to 9 and 21 to 29 (each minus an interspersed nuculid layer -- 7 and 23). McCollum considers the first group a Lingula assemblage and the second as part of the Devonochonetes-Retispira subassemblage. McCollum's is primarily a sedimentological analysis where identification of assemblages is secondary to environmental description. My approach, on the other hand, has been to focus on the fauna and the identification of community types.

There is no clear choice as to approach here. Taphonomic issues make primary reliance on fossil counts obviously problematic. However, in spite of the vaunted stability of the Hamilton environment, characterizing up to several meters of sediments within one environmental regime has its limits as well when community types are to be described in detail. Since McCullom separately sampled interspersed layers (such as the recurring nuculid layers) -- see Table 4.11, finer tuning of the 1/2 meter sampling units may not result in substantially different characterizations. The issue of "matting" (McCollum, 1980) of "Leiorhynchus" and other species may need further investigation.

There is also a potential problem of trophic-mobility-substrate characterization. McCollum considers "Leiorhynchus" to be pelagic or epiplanktic while I have considered them to be epibenthic suspension feeders (see also Vogel, Golubic and Brett, 1987). To change my characterization would result in a shift of niche type for the "Leiorhynchus"-Devonochonetes community type. Of interest here is that the multivariate analysis allows one to separate the "Leiorhynchus"-Devonochonetes and the Devonochonetes-Ambocoelia community types. This separation also occurs between niche groups (Table 4.10) and at the Alden-Elma boundary in the Buffalo Creek-Caughels Creek area. This separation of the community types remains even when the dominant species for each type is removed. This removal includes the potentially problematic "Leiorhynchus", the dominant species of its community type.

2. Community Types in the Biofacies and Depositional Environment of the Hamilton

McCollum (1980) discusses in detail the depositional environment of her sample. This description and analysis is generally consistent with the paleoecological model (Figure 4.8) developed by Brett and Baird over the last several years for the upper Hamilton (e.g., Brett, Baird and Miller, 1986 and Vogel, Golubic and Brett, 1987).

The community types described in this chapter probably occurred in low aerobic to somewhat dysaerobic environments (some 30 to 100 meters in depth -- Brett, Baird and Miller, 1986). Changes in community type were governed by physical and biological environmental factors -- the most important biological factor being bioturbation.

In the Buffalo Creek-Caughels Creek area, during the deposition of the Alden shales, there occurred a "Leiorhynchus"-Devonochonetes community type. If the often matlike occurrence of "Leiorhynchus" (McCollum, 1980) indicates a separate assemblage from the other fauna, then there may have been relatively short term and regular cycling between Brett and Baird's type 1 and type 3b biofacies throughout the Alden in this location. In a less turbid setting during the succeeding Elma there occurred a Devonochonetes-Ambocoelia community type. It would be placed in type 3a biofacies. Succeeding this in the Elma were the diminutive brachiopod type 2 biofacies which included examples of the Ambocoelia-Tropidoleptus, Tropidoleptus-Truncalosia, and Devonochonetes-Ambocoelia community types. Interspersed on a fairly regular basis throughout these Alden and Elma community types was the nuculid community type occurring in a setting of high bioturbation and consequent increased turbidity (McCollum, 1980). This would be placed in biofacies type 3b.

Occurring to the east near Darien Center for a portion of the Elma was the Ambocoelia-Craniops-trepostomate community type. It is difficult to assign it a biofacies type when considering the different environmental requirements of the above named dominant species as well as the consistently present and diverse nuculids that are also found in this community type.

Near the top of the Hamilton, in the Moscow Windom, there occurred, along the shore of the present-day Lake Erie, an Ambocoelia-Tropidoleptus community type. Again, there appears to be no clear biofacies type within which to place this.

Finally, in the Chenango Valley of central New York, there occurred during the Moscow Windom the Chonetes-

Ambocoelia community type with *Mucrospirifer* and nuculids, among others, common. It would seem to indicate a somewhat turbid setting of biofacies types 3a and 4b. At one point, large numbers of bryozoans appeared in this community type indicating a change to a less turbid environment. In these same bryozoan sampling units, the infaunal nuculids are approximately half as abundant as they are in the other sampling units of this community type. It is this set of changes, among others, that led to the modeling effort discussed in Chapter 6.

CHAPTER 5: STRUCTURE: COMMUNITY AND POPULATION BASES

Introduction

The purpose of this chapter is to evaluate population level and community level contributions to community structure. Following this introduction, the methodology to be employed will be introduced along with a discussion of its relevance and limitations when used in a paleoecological study. Then, two community types (chosen from those identified in Chapter 4) will be introduced and commented upon.

The subsequent section consists of a Monte Carlo numerical analysis in which Randomly Generated Data are compared to Field Data in an attempt to identify structure. Subsequently, the population and community components to this structure will be sought. The patterns identified as a result of the various multivariate and other analyses undertaken in Chapter 4 do not constitute proof of community level contribution to structure. That was a descriptive effort and there is a distinction to be made between descriptive patterns and functional structure established for a *particular* hierarchical level.

Since the essential measure of structure employed is based upon relative "invariance" (Lane, Lauff and Levins, 1975) -- consistency or predictability -- there will be a discussion of the relationship between invariance and structure.

The Use of Macroscopic Parameters of Natural Ecosystems

In a study of the plankton of Gull Lake in Michigan, Lane, Lauff and Levins (1975) and Lane and Levins (manuscript) attempted to identify macroscopic (community level) parameters, elucidate the invariant or consistent relationships of those parameters under different conditions, and demonstrate predictable changes as the system changed. In short, they wished to identify community structure beyond the simple summation of population parameters. They argued that "Macroscopic properties constitute quantifiable descriptors of communities and ecosystems that delineate whole-system properties" (Lane and Levins, manuscript).

Community structure refers to the extent of population interdependence. Greater interdependence is indicated by a stronger structure (Pielou, 1972). However, populations (and abiotic components) do make their own inherent contributions to community structure. It then becomes important to distinguish between community and population contributions to structure -- the major intent of this chapter.

The development of macroscopic parameters has been derived from niche work, especially as in Levins' (1968) "Theory of the Niche". Since only sampling unit (sensu Pielou, 1984) population abundances are required to calculate the various measures, the exploration of the possible usefulness of this approach with regard to the fossil record is worthwhile. Significantly, the importance of competition in determining structure and that the sampling units (in this theory, habitats) "adequately represent the distribution of species" (Lane, personal communication) are two fundamental assumptions.

Competition, no matter how reasonable a biological assumption, is difficult to demonstrate (see Chapter 2). This is especially so in studies of the fossil record. However, it is possible to view the alpha, otherwise termed competition, matrix that is an important part of the Theory of the Niche as a matrix of the probability of co-occurrence. This less strictly competition-centered co-occurrence matrix is most appropriate to use with populations that are "habitat selectors" (Lane, Lauff and Levins, 1975) and occupy a broadly similar functional role. In this study, my own interpretation is that only populations of the same trophic, mobility and substratum groups should be used in such an evaluation.

The sampling units of this study are grouped according to patterns suggested by the multivariate and other analyses described in Chapter 4. As in neoecological sampling, no definitive assurance that population distributions in the sampling units are an appropriate representation of the living distributions is possible. However, the temporal and spatial patterns as determined in Chapter 4, the use of less than half of the original sampling units as appropriate for this particular evaluation, and the requirement that only the most abundant populations be included all indicate the appropriateness of the macroscopic approach for this particular study of the fossil record.

Lane and her co-workers combined their abundance data with a series of physical-chemical measures determined at the sampling unit level. Consequently, they were able to undertake a rich analysis of the implications of the changes in community structure observed over the seasons and, because of eutrophication, over a period of years. The detailed microstratigraphic environmental data gathered for each sampling unit as used by Lane et al. is not available for this study and would require an approach like that advocated by Schindel (1980, 1982) in order that the potential of the macroscopic approach advocated by Lane and her co-workers be fully realized in an analysis of the fossil record. Such sedimentological, stratigraphical, and geochemical analysis undertaken for each sampling unit was never intended to be part of this study. It is, unfortunately, all too rare in paleoecological work in general.

Of more immediate concern in arguing for the value of this neoecological method for paleoecological application is the question of statistical appropriateness. The statistical validity of the macroscopic approach has not as yet been evaluated. Given that macroscopic biotic evaluation has usually been placed within an overall environmental study, the lack of statistical work is understandable. However, especially given the attempt to introduce this method into paleoecological analysis, now is an appropriate time to undertake a statistical evaluation of the method. In this method, community level phenomena are judged as important considerations in an ecological study to the extent that they are more "invariant" than equivalent population level phenomena. As a review of the equations (see below and Appendix 5.1) used in this study will show, macroscopic (community) parameters are essentially averages of the component population results for the relevant sampling units. We might, therefore, expect the community level averages to be more invariant than the population parameters simply because of this averaging. In this study a Monte Carlo simulation has been undertaken and results compared to the measures based upon the actual fossil data. The comparison permits an evaluation of the significance of the macroscopic approach. This is the first time this method has been subjected to any kind of numerical analysis.

The Monte Carlo analysis also allows me to address an important paleontological question. Irrespective of whether any perceived structure is primarily population or community level in origin, there is the question of whether the fossil sample indicates <u>any</u> structure at all. Given all the possible taphonomic biases that stand between death and discovery, there is the very real issue of the relationship of the sampled fossils to the original living structure. A comparison of the results of the analysis of a series of community and population measures for the sampled fossils, and a series of randomly created data sets, allows me to address the prior question of the existence of structure. If a structure is found, the attempt to distinguish between relative population and community level contributions can be made. I am not presuming upon the patterns elicited as a result of the analysis reported in Chapter 4. In searching for structure by employing methods based upon neoecological population dynamics, any positive results will give confidence that, despite possible taphonomic distortions, some component of the original structure is preserved.

I am greatly indebted to Dr. Dwight Kincaid of Lehman College for his help and interest in the creation of the appropriate computer programs.

The Use of Community and Population "Niche" Equations

The eighteen equations and their definitions as used in this chapter are listed in Appendix 5.1. Their source is Lane, Lauff and Levins (1975) and Lane and Levins (manuscript). In two instances (equations 15 and 16) there are modifications which are indicated but not clearly specified in these references. The procedure involves the grouping of sampling units (<u>h</u>abitats) [underlining a letter refers to appropriate term in the equations listed in Appendix 5.1.] into macrohabitat groups (<u>e</u>nvironments) and the scoring of values for a particular measure from environment to environment across the full community sample. Thus, each sampling unit is considered a habitat, a group of sampling units (e.g., sampling units from the same bedding plane, taxonomic layer, etc.) is considered an environment, and a sequence of these environments is considered a community (see Figure 5.1).

In the evaluation of whether or not community level parameters are epiphenomena of population level parameters, there are three relevant comparisons to be made:

	population measures	community measures
1)	relative niche breadth (eq. 7)	average relative niche breadth (8)
2)	co-occurrence success ratio (13)	average co-occurrence success ratio (14)
3)	utilization efficiency ratio (15)	average utilization efficiency ratio (16)

The first pair of measures are classic niche breadth measures adjusted for number of habitats (sampling units). The second pair measure population effects included in the community (environment) matrix. The third pair measure population and other environmental effects outside of the community (environment) matrix. (See Lane, Lauff, and Levins, 1975, for further discussion.)

The question of relative population and community level contributions to structure is addressed by comparing the relative invariance of the measures within each pair across the environments and thus for the community type.

In this study the intent with respect to the use of these three particular pairs of measures is rather resticted, for reasons noted above. It is aimed at an initial exploration of fossil community structure and, possibly, a determination of the degree to which community level properties contribute to such a structure. The efforts reported in this chapter constitute one of three major investigative thrusts of the study as a whole, with the community descriptions and hierarchical investigations of Chapters 4 and 6, respectively, constituting the other investigative efforts. Thus, it is not the purpose of this study to explore in depth the biological meaning of the results of the various analyses (however, see below). Such an exploration would best be done in the context of environmental data established at the sampling unit level along with other relevant measures including the community niche breadth (eq. 9), the average overlap value for the community (alpha) matrix (11), and the total community diversity (18).

The Choice of Community Types and Sampling Units

This evaluation of community and population components of structure was undertaken with two of the community types identified in the analyses of Chapter 4. The two selected community types are the "*Leiorhynchus*"-*Devonochonetes* of the

Ludlowville Ledyard and the Chonetes-Ambocoelia of the Chenango Valley, Windom. Appendix 5.2 gives the sampling units chosen and the populations used for this part of the study.

This selection of community types was made for the following reasons:

1) At the subgroup (environment) level: Each community type can readily be broken down into subgroups of macrohabitats (environments) required by the method used. The sampling units of "Leiorhynchus"-Devonochonetes probably cover some hundreds of thousands of years. Regularly, it is "lost" as the nuculid community type replaces it. Between each cycle of the nuculid community type a series of closely associated sampling units -- subgroups or environments -- are found (see Table 5.1 and Chapter 4 for criteria used in grouping these sampling units).

The Chonetes-Ambocoelia community type probably encompasses only some few thousands of years. The required grouping of habitats can readily be made by matching sampling units (such as those from the same bedding plane or bryozoan layer), taken from quarries in the same vicinity, which were deposited at essentially the same time. These resultant subgroups (environments) are composed of closely associated sampling units (see Table 5.1 and Chapter 4).

2) At the community level: The two chosen community types are themselves each composed of closely associated sampling units (see Table 5.1 and Chapter 4). Thus, there are

groupings of sampling units (habitats) into environments which are themselves grouped into readily distinguishable community types as identified and described in Chapter 4. 3) The dominant populations of each community type are relatively few and are epibenthic, low (attached or immobile), suspension feeders (see Appendix 5.2 and Table 1.3). In the "*Leiorhynchus*"-*Devonochonetes* community type, five such populations make up 94% of the over 11,000 fossils counted. In the *Chonetes*-*Ambocoelia* community type, eight such populations make up 89% of the over 6,000 fossils counted.

Less than half of the sampling units described in Chapter 4 and only two of the seven community types identified were deemed suitable for the structural analysis reported in this chapter.

The Existence of Structure: Monte Carlo Evaluations

Is there any structure indicated by the data? Two Monte Carlo approaches are used (see Appendix 5.3): a Coefficient of Variation analysis and a raw number analysis.

The measures evaluated are:

population

1) relative niche breadth (eq. 7)
2) co-ocurrence success ratio (13)
3) utilization efficiency ratio (15)

community

4) average relative niche breadth (8)

5) average overlap value (11)

6) average co-occurrence success ratio (14)

7) average utilization efficiency ratio (16)

8) total community diversity (18)

1. Coefficient of Variation Comparison

The Coefficient of Variation values of the Field Data can be ranked within sets of Randomly Generated Data for each of the eight measures. The Randomly Generated Data is based on similar column (sampling unit) totals to those of the Field Data (see Appendix 5.2). Population number (five for the *"Leiorhynchus"-Devonochonetes* community type and eight for the *Chonetes-Ambocoelia* community type) and environment groups are arranged to correspond to the Field Data. Thus, random numbers have been generated for each of the populations for each sampling unit and the total has been set to equal the actual total organism count per sampling unit of the Field Data.

Ninety-nine sets of Randomly Generated Data were created for each population for the three population measures and for each community for the five community measures for each community type. Included with the Randomly Generated Data values was the Field Data based value for the relevant measure. A Coefficient of Variation evaluation was undertaken for each of the resulting one hundred sets. The purpose here is to see how (for any given measure) the Field Data based Coefficient of Variation is distributed among the 99 random number based Coefficients of Variation. Is the variability found in a particular measure for a population or community component surprising or distinctive when compared to expectations based on the Monte Carlo simulation? In this sense, either a high or low Coefficient of Variation for Field Data based measures is meaningful _if_ it is at the end of the distribution.

A word needs to be said about considering high Coefficient of Variation values as potentially indicative of structure. For instance, alternating very high and very low raw values will give a relatively high Coefficient of Variation _and_ indicate the possibility of structure. Similarly, in a correlation study, an r_{xy} of 0 indicates no linear relationship between the variables. There may, however, be a strong non-linear relationship and a high degree of predictability as would be the case when considering a parabola (Suzuki, Griffith, and Lewontin, 1981). Invariance (or a low Coefficient of Variation) is but one aspect of structure even if among the most striking and readily interpretable.

Where a Field Data based Coefficient of Variation value is high in comparison to Randomly Generated Data based values, it should not be dismissed as being uninformative with respect to structure. One important aspect of perceiving structure is that, whatever values one determines from various measures, they are not reproducible from a Monte Carlo analysis. Measures of variation and randomness are not necessarily one and the same thing. Standard Deviation and Variance are measures of dispersion, not randomness. Wilson (1975) accepted greater than random dispersion values as indicators of pattern in his group selection model.

Table 5.2 for the "*Leiorhynchus*"-*Devonochonetes* comparison shows that the Field Data Coefficient of Variation value for twelve of twenty comparisons is either one of the lowest or highest five of the 100 sets of data (ninety-nine randomly generated and one from the field data). This includes nine values that are either the lowest or highest score. These values account for eight of fifteen of the population measures and four of five of the community measures.

Table 5.3 for the *Chonetes*-*Ambocoelia* comparison shows that the Field Data Coefficient of Variation value for sixteen of twenty-nine comparisons is either one of the lowest or highest five values of the 100 sets. This includes eleven values that are either the lowest or highest score. These values account for thirteen of twenty-four of the population measures and three of five of the community measures.

2. Raw Number Comparison

A second type of Monte Carlo evaluation is also possible: in addition to comparisons of Coefficient of Variation results of Randomly Generated Data and Field Data, a comparison can be made of the _actual_ values for each of the various measures taken at the environment level (four of the _"Leiorhynchus"-Devonochonetes_ community type and six of the _Chonetes-Ambocoelia_ community type -- see Table 5.1 and Appendix 5.2). Sets of ninety-nine Randomly Generated Data were established for each measure (twenty for the _"Leiorhynchus"-Devonochonetes_ community type simulation and twenty-nine for the _Chonetes-Ambocoelia_ community type simulation). The actual results obtained from the Field Data for the particular measure were then compared with the ninety-nine results derived from the Randomly Generated Data.

Table 5.4 shows that nearly 57% (146 of 254) of the Field Data measures are either one of the lowest or highest five for the set of 100 for a given measure. This figure rises to more than 80% (42 of 50) in the community level measures. In addition, over 40% (103 of 254) of the total measures and over 60% (31 of 50) of the community level measures of the Field Data lie outside of the range of the Randomly Generated Data; they are either the lowest or the highest score of the combined set of 100 values for the relevant measures. In general, the _"Leiorhynchus"-Devonochonetes_ Field Data values are more distinctive than those of _Chonetes-Ambocoelia_, but, there is no significant (however, see below) difference between the community types regarding proportion of low or high values.

Table 5.5 is a breakdown by type of measure and by similated community type. While the majority of values of the Field Data measures which are distinctive are at the low value end, a full one-quarter are at the high value end. Of these values, 88% (37 of 42) of the community scores are at the low end while 70% (73 of 104) of the population scores are at the low end. There is a greater tendency for population values rather than community values to be distinctive by virtue of a relatively high value in comparison to Randomly Generated Data (see below).

In spite of taphonomic, sampling and methodological biases there appears to be considerable population and community level structure (as measured by unusually low or unusually high variability) to be found in the two community types. A considerable degree of non-overlap exists between the Field Data and Randomly Generated Data. This conclusion may be obvious, and, in fact, Chapter 4 is a concerted attempt to elucidate structure (without attributing its causes). Nevertheless, given that we are dealing with the fossil record and, in the present chapter, applying a neoecological method, it is useful to establish the appropriateness of the efforts described for a paleoecological study. Each community type does have numerous non-random patterns as evidenced by the two different types of analysis and it is appropriate to evaluate the community and population level contributions to the structure.

Community and Population Level Contributions to Structure

Lane and her co-workers, in their neoecological studies, calculated values for relevant population level and community level measures and compared the results by evaluating graphs of these values for a particular measure. By looking at the graphs of values scored from environment to environment they established relative invariance. In this study, in addition to using graphs (see Figures 5.2 and 5.3), I have also prepared Tables (5.6 and 5.7) which give the actual values obtained for each measure for each environment and the Coefficient of Variation of the values within each measure. Coefficient of Variation values -- the indicator of relative invariance (Simpson, Roe and Lewontin, 1960) -- can be determined at the population and community levels for a series of measures. These values, when low, suggest the relative invariance from environment to environment within each community type and can be considered an indicator of structure. I am using the Coefficient of Variation for the relevant population and community measures as the ultimate basis for my decisions on relative invariance. The reasons for using Coefficient of Variation rather than Standard Deviation for recognizing invariance are that there is a scale difference between population and community components and that the use of Standard Deviation tends to minimize contributions of the more abundant populations. The overall result using a Standard Deviation measure in this particular study would be to de-emphasize population contributions to structure and emphasize community contributions.

The issue here is, having established the existence of structure (the above discussed Coefficient of Variation and raw data analyses each undertaken with a random number comparison), I now wish to distinguish between population level and community level contributions to the structure inherent in these community types. It is here that a low Coefficient of Variation value has special meaning for the particular method employed.

Tabel 5.6 and Figure 5.2 report the results for the "Leiorhynchus"-Devonochonetes community type. The average Coefficient of Variation rank for the three sets of compared measures is 1.3 (maximum of 6) for "Leiorhynchus", 2.3 for the community, and 2.7 for Devonochonetes. The dominant population ("Leiorhynchus") is more invariant than the community values for the compared measures, and the second most abundant population (Devonochonetes) is nearly as invariant as the community values. The community level measures, although invariant, are not the most invariant. The ranking of population and community measures for Coefficient of Variation is useful for establishing relative rankings of variation. However, only those with a low Coefficient of Variation can actually be thought of as invariant. For this type of data, a Coefficient of Variation of less than 15% is considered relatively invariant. This is higher than is usually acceptable for morphological data (Simpson, Roe, and Lewontin, 1960). However, for population and community data, and paleoecological at that, higher values appear acceptable. In addition, there is a clear gap around the 15% value. In the "*Leiorhynchus*"-*Devonochonetes* community type, the highest below 15% value for the three sets of measures averages 8.3% while the lowest above 15% value averages 22.4% -- a 14.1% gap. Five of the eighteen measures, including two of the three community level measures, show a Coefficient of Variation of less than 15%.

Table 5.7 and Figure 5.3 report the results for the *Chonetes-Ambocoelia* community type. The average Coefficient of Variation rank for the three sets of compared measures is 1.7 (maximum of 9) for *Chonetes*, 2.7 for the community, and 3.3 for *Cyrtina*. Here, again, the dominant population is more invariant, and a not particularly abundant population (*Cyrtina*) is nearly as invariant as the community values. The community level measures, although invariant, are not the most invariant. As with the "*Leiorhynchus*"-*Devonochonetes* community type, there is a clear gap around the 15% Coefficient of Variation value and those below this value are considered invariant. For the *Chonetes-Ambocoelia* community type, the highest below 15% value for the three sets of measures averages 8.9% while the lowest above 15% value averages 20.1% -- an 11.4% gap. Ten of the twenty-seven measures (including the three community level measures) show a Coefficient of Variation of less than 15%.

Discussion

The study results show that there is considerable invariance or consistency (as well as other measures of structure -- see below) in the measures at both the community and population levels. The invariance in measures of niche breadth, co-occurrence, and utilization efficiency ratios are likely to have some relationship to the sampling units being grouped at the onset as a community type. The initial grouping into community types (as noted in Chapter 4) constitutes an identification of patterns. Whether such community types have structural characteristics depends upon identifying population and community level contributions to pattern using functionally-based measures of structure. The efforts of this and the succeeding chapter are aimed at elucidating such possible functional contributions to structure. In this chapter, the measures undertaken and evaluated are niche breadth, co-occurrence success ratio (population effects included in the community matrix), and utilization efficiency ratio (population and other environmental effects outside of the community matrix). These measures are based upon functional assumptions of population neoecology. The results of the Random Generated Data evaluations also support the conclusion. More importantly, I would expect patterns distinguished as a result of the multivariate and other analyses described in Chapter 4 to be supported by the analysis reported in this chapter -- an independent approach (although still within an ecological framework (Pilette and Salthe, 1985)). In other words, the invariance (see below for a final discussion of the relation between invariance and structure) demonstrated in the various community and population measures tends to support the conclusions of Chapter 4, and lends robustness (Levins, 1966) to the whole enterprise.

There still remains the question of population versus community level contributions to the perceived structure -- in this study, the invariance found in numerous measures. Firstly, the question is not of an either/or kind. In Chapter 2, I described and concurred with the suggestions of more encompassing community perspectives (Kauffman and Scott, 1976 and Levins and Lewontin, 1980) that alternative community views should not be mutually exclusive. Accordingly, one ought to measure various attributes appropriate to abiotic, population and community characteristics, and attempt to explain the relationships, or lack of, found. The proviso is, of course, that the contribution from a particular characteristic (or our perspective of it) is reasonably important.

This study is not complete and it is not a local-ecosystem investigation. Physical-chemical environmental information is not available at the sampling unit level. However, there are important questions raised about community level and population level contributions to the perceived community structure. The importance of population level contributions to community structure is generally accepted and has been addressed in Chapter 4 in the context of community type. It is also seen in this chapter with the important relative invariance of two populations found in each community type. Also significant is the considerable nonrandomness of the population measures in general (104 of 204 or 51% -- see Table 5.4).

In addition to the relative invariance of the dominant population for each community type -- a not completely unexpected result -- invariance also characterizes *Cyrtina* in the *Chonetes-Ambocoelia* community type. A not particularly abundant population, *Cyrtina* comprises less than 2% of the sample for the sampling units used in this analysis. Neither in the analyses undertaken in Chapter 4, nor in multivariate analysis applied solely to the sampling units used in this chapter does *Cyrtina* stand out. However, the search for structure undertaken in this chapter has enabled identification of the *Cyrtina* population as significant despite its relatively low abundance. Thus, by means of this analysis of structure I find population phenomena not evident in other analyses, including multivariate analyses. A multifaceted approach is clearly of value.

Is the community level contribution important? There is considerable nonrandomness of the community measures in general and the following observations can be made:
1) For measures of relative niche breadth (7 and 8) the community Coefficient of Variation value for the Field Data falls well within the range of the Randomly Generated Data for both community types. The Field Data value is very close to the mean value for the Randomly Generated Data in both cases. Although the community value is relatively invariant in both community types, there are populations (one for the "Leiorhynchus"-Devonochonetes community type and two for the Chonetes-Ambocoelia community type) with more invariant values. Thus, the community value does not indicate either structural importance or particular community level significance in either community type examined for relative niche breadth.
2) For measures of co-occurrence success -- population effects included in the community matrix (13 and 14) -- the community Coefficient of Variation value for the Field Data is lower than any of the ninety-nine Randomly Generated Data values for the Chonetes-Ambocoelia community type and is lower than all but four of the Randomly Generated Data for the "Leiorhynchus"-Devonochonetes community type. The community values are also extremely invariant, much more invariant than any of the population values. The commmunity value indicates both structural importance and community

level significance for both community types examined for co-occurrence success.

3) For measures of utilization efficiency -- population and environmental effects outside of the community matrix (15 and 16) -- the community Coefficient of Variation value for the Field Data is higher than any of the ninety-nine Randomly Generated Data for both community types. The *Chonetes-Ambocoelia* Field Data value is invariant while the *"Leiorhynchus"-Devonochonetes* value is not. In both instances, there are three populations with more invariant values. The community value indicates structural importance but not community level significance for each community type (especially for *"Leiorhynchus"-Devonochonetes*) examined for utilization efficiency.

Along with the real structure observed in the Field Data at both the population and community levels there is both population and community level significance. Important portions of this analysis require community level interpretations. There are, for both fossil community types investigated, community level (macroscopic) parameters that are not mere epiphenomena of population level parameters.

Lane and her co-workers extended their neoecological analyses beyond what I have been able to undertake in this study. They evaluated patterns within the community type which related to changing values of relative niche breadths (7 and 8), co-occurrence success ratio (13 and 14), and utilization efficiency ratios (15 and 16), at both the community and population levels. They also investigated the community level significance of changing values for community niche breadth (9), average overlap value (11), and community diversity (18). In order to undertake a discussion of these parameters, which includes the abiotic environmental context, appropriate physical-chemical measures taken at the sampling unit (habitat) level must be made.

Biological discussion incorporating relevant abiotic, population, and community characteristics represents a local-ecosystem analysis -- an analysis centered in the functional hierachy discussed in Chapter 3. Without the accompanying environmental data any analysis is abstracted from the abiotic hierarchy and is, accordingly, an investigation centered only in the biotic hierarchy -- such as that reported in this study. Paleontologists are, however, in a position to add appropriate environmental data at the sampling unit level as advocated by Schindel (1980, 1982) with respect to microstratigraphic analysis.

In a paleoecological investigation, a study of the "Leiorhynchus"-Devonochonetes community type is as appropriate as one of the Chonetes-Ambocoelia community type. A time span of hundreds of thousands of years is as appropriate as one covering a few thousands of years. In either case it is important to establish the existence of patterns describable in terms of a community type with strong within-type correlations and between-type distinctions, patterns which emerged in the analyses undertaken in Chapter 4. In addition, a Random Generated Data evaluation of the significance of these patterns ought to be undertaken. Paleoecologists could, then, contribute to our understanding of communities by incorporating abiotic, population and community phenomena into their discussions of community structure, and by considering these phenomena within the context of evolutionary significant periods of time.

Finally, the question of invariance with respect to structure needs to be addressed. Several issues are involved: stability versus resilience, descriptive pattern versus functional structure, distinctiveness versus randomness.

For a local-ecosystem and its associated community, a functional characteristic that I am interested in is degree of persistence. This is especially true when studying paleosystems. The interplay of stability and resilience (see Chapter 2) is an important consideration. More stable systems tend to be less resilient and vice versa (Holling, 1973). Placing the results of this study within the framework of stability-resilience theory may be helpful. In this study, I consider relatively invariant measures, such as indicated by a low Coefficient of Variation, as an indicator of stability. The proportion of middle and high Coefficient of Variations <u>may</u> be an indicator of relative resilience within a system. Those high values which also possess pattern may contribute more to stability than middle and high random values and may contribute more to resilience than low values. Invariance may very well be a measure of degree of short-term structure or stability. More variable results may be a measure of long-term structure or persistence as long as nonsupportable degrees of randomness are avoided. A community in order to persist in time requires a proper mix of stabilizing and resilient populations. Without the former, a community may very well not be able to exist at a given point in time. Without the latter, it may not be able to persist for any given length of time.

Two additional points may be made with respect to stability and resilience. First, the degree of environmental variability over time will affect the relationship between stability and resilience (Odum, 1971). A consistent predictable environment will encourage relatively more stabilizing populations and communities that are relatively more stable. Less predictable, but not disfunctionally random, environments should encourage more resilient populations and communities -- less stable but more persistent.

The community types evaluated in this study may be compared with respect to these considerations. Two out of the three community level measures and three of fifteen (20%) of the population level measures are invariant for the "Leiorhynchus"-Devonchonetes community type. All three community level measures and seven of twenty-four (29%) of the population level measures are invariant for the *Chonetes-Ambocoelia* community type. *"Leiorhynchus"-Devonochonetes* is a relatively long-term persistent community type -- cycling throughout the Ludlowville Ledyard (Alden -- McCollum, 1980) Member of the Hamilton (see Chapter 4). *Chonetes-Ambocoelia* was deliberately studied as a short-term sampling regime. However, it seems to first appear near the top of the Windom Member and certainly does not persist past the Windom. (Community types here are tightly defined based on the analysis reported in Chapter 4 and should not be confused with the sometimes looser identification of community types sometimes found in paleoecological literature.) It just may be that the *"Leiorhynchus"-Devonochonetes* community type is less stable but more resilient than the *Chonetes-Ambocoelia* community type. It is a prediction worthwhile investigating. At this point, a caveat needs to be noted for I have been comparing community types based upon different sampling regimes and from different Members of the Hamilton. This and taphonomic issues render the attempt a difficult one -- but not less worth the undertaking.

The second additional point concerning stability and resilience is to focus on population activities: populations interact with and change their environments (function circles -- see Chapter 3), populations change their roles with respect to stability (Pilette, Blamire, and

Sigal, in press), and destabilizing populations can be necessary to the short-term functioning of a community. Concering this last point, I have modeled published community interaction matrices and found that removal of destabilizing populations can lead to community collapse. No community is particularly coherent in the short- or long-term if it does not include a relevant mix of stabilizing and resilient populations. What is a relevant mix depends both upon the environment and the nature of the population interactions both of which can and do change -- see Barkai and McQuaid (1988) for a documented example of predator-prey reversal.

The descriptive patterns that we "observe" as a result of the application of particular methodologies is not one and the same with functional structure. However, for science, the connection to functional structure can only be made via establishing patterns or (as described in Chapter 6) making correct predictions. The limits to the descriptive exercise reported in Chapter 4 is not that it is a descriptive exercise but that the patterns discovered could not be apportioned between the population and community levels. Since there is little debate among ecologists regarding population (and abiotic) influences upon community structure, the issue really revolves around the community level component involved. This is the rationale for the efforts described in this chapter.

It is clear from the results reported here that there are many community level components to the structure seen in the two community types investigated. Certain phenomena cannot be ascribed to population level components, and, it is hard to imagine that abiotic explanations would suffice.

The Random Generated Data exercises go some way to establishing a link between functional structure and descriptive pattern. Overall, more than 50% of the various measures cannot be reproduced with a Monte Carlo approach. They would seem to exist because of some set of relationships, i.e., functional structure, in the community. Many of these are community level relationships in addition to the expected population level ones. What is important is the uniqueness of the Field Data.

The distinctive high Coefficient of Variation values tell us something about the functioning of the community. (It is interesting, and worth investigating, that there is a disproportionate number of population measures compared to community measures that are distinctive and high.) But, they are not helpful regarding invariance. Measures of invariance are not equivalent to measures of structure -- they are a component of structure, perhaps the component relating to relative stability. The complexity of community structure involves stability and resilience and includes populations with different roles for these (and other) phenomena. Anything less probably wouldn't last through the normal developmental cycle (or cogent moment) of the local-ecosystem let alone last long enough for community evolution to take place. On the other hand, these local failures would affect specific demes and may play a role in population evolution.

CHAPTER 6: THE USE OF LOOP ANALYSIS IN A HIERARCHICAL CONTEXT

Introduction

Loop analysis, as developed by Levins (1974 and 1975), takes advantage of "the equivalence between differential equations near equilibrium, on the one hand, and matrices and their diagrams, on the other" (Levins, 1975). Appendix 6.1 is an overview of the loop analysis method and Appendix 6.2 outlines basic underlying assumptions in its use.

Loop analysis has been used in a variety of ways:
a) in a broad heuristic sense to reinforce arguments calling for consideration of indirect effects on communities (Levins, 1975);
b) as a minor component in the formal mathematical treatment of various other topics (Demetrius, 1977);
c) for direct study on system level questions including community stability evaluations, role analysis, and relationships between stability and complexity (Lawson, 1977; Lane, 1986 and Pilette, Sigal and Blamire, 1987); and,
d) to evaluate treatment or perturbation (parameter change) effects of an entity on itself and on the other entities in a system (Briand and McCauley, 1978; Puccia and Levins, 1985 and Lane, 1986).

Lawson's work (1977) may represent the only use of loop analysis on fossil data to date. Lawson evaluated the stability of relatively large marine invertebrate fossil communities (fifteen to twenty populations -- entities) using the technique of loop analysis and concluded that there was no significant taphonomic bias of the trophic stability evaluations for the communities studied.

Lane's work represents the only consistent attempt to construct relatively large community systems using loop analysis. Lane is attempting to discover which parameter change, when applied to a possible loop digraph, will generate a "prediction", consistent with empirical sampling, of a change in numbers for an entity (population, guild or nutrient in Lane's work). This change is at the level of signs (positive, negative or no significant change). For instance, from week 4 to week 5 in a sampling regime on Long Island Sound, the numbers of the various algae, zooplankton, and other entities have been observed to change. Lane seeks to find which loop digraph and parameter change will generate the observed sign changes.

Loop Analysis and the Hamilton Sampling Units

Loop analysis is relevant in studies of the fossil record because changes in numbers are observed from sampling unit to sampling unit for various fossil populations. However, the technique presupposes a meaningful connection between the sampling units. Lane, for example, uses data taken from sampling units, on a weekly or monthly basis, in the same part of the water column. We should, if wishing to study the fossil record using loop analysis, be able to make a minimal assumption of temporal and geographic relationships; avoid obvious breaks such as unconformities and storm events; and avoid sampling units which extend over relatively long periods of time or which contain evidence of different environmental regimes.

The sampling units in this study suggest a reasonably good situation with respect to the concerns expressed above. The Windom sampling units from the Chenango Valley have been taken, without breaks, in 10 cm increments. Given the considerable thickness of the Hamilton strata in the Chenango Valley -- probably over 300 meters -- and the gross sedimentology of the Windom, 10 cm probably represents from a few hundred to a very few thousand years. The microstratigraphic work advocated by Schindel (1980 and 1982) can obviously be useful in making more accurate estimates of time periods.

As observed in each of three quarries within a 5 km radius of one another in the Chenango Valley, there are empirically observed significant changes in numbers for several of the most abundant populations from one sampling unit to the next (Table 6.1). These sampling units are grouped into the Chonetes-Ambocoelia community type. Multivariate and other analyses reported upon in Chapter 4 and the structural analyses reported upon in Chapter 5 support the grouping of these sampling units in one community type. The raw data used in Table 6.1 is presented in Appendix 6.3 while Appendix 6.4 refers to how the data was scored.

The above information has been used in the construction of a digraph, the perturbation (parameter change to one entity) of which will generate these observed sign changes in population and/or guild numbers. This type of modeling effort is significant in itself and has been used by various investigators as a basis for discussion of both the ecological attributes of the models and the insights into communities and ecological theory that they may generate.

However, the digraph or system generated in this, or any, modeling process does not necessarily represent an objective community. In fact, recent investigations, especially that of Taylor (1985 and personal communication), makes it clear that community matrix work, in general, models solely "apparent interactions". The modeled interactions are a stand-in for the actual ecological interactions and it is quite possible that the latter bear little resemblance to the former. With this limit in mind, it is, nevertheless, possible to use community matrices in ecological investigations. For instance, Lane (1986), in a regime of multiple sampling and careful attention to biological detail, has constructed and used large digraphs in a meaningful manner.

However, discussions concerning community reality are still necessarily subjective. To render the question an objective one we must ask if a community matrix can be used to predict effects seen at other hierarchical levels -- levels different than those incorporated explicitly in the model. Such predictions would be especially telling if they were unmatched or not as parsimoniously generated at the more traditional ecological levels of the organism or population. My study of fossil data makes just such a test possible.

Predicting Turnover Rates

Lane and Levins (1977), and Puccia and Levins (1985) discuss the potential of loop analysis to predict turnover rates for an entity in a system. In ecological situations, turnover rates are defined as "the reciprocal of life expectancy of an organism..." (Puccia and Levins, 1985). Thus, for example, if the turnover rate is expected to increase, the age structure of a population should shift to the younger end. Turnover rate predictions have never been tested in either neoecological or paleoecological situations. This study represents the first empirical application of the procedure.

With suitable fossil populations, a turnover rate prediction can be made with fossil data. Specifically, a *Sulcoretepora gilberti* layer of less than 10 cm thickness was observed in each of Geer Road, Lebanon Center Road and Deep Spring Road quarries. From other observations (see Figure 4.1 and accompanying discussion) it was clear that the *Sulcoretepora* layers matched and, given the less than 5 km radius between the three quarries, they probably are of nearly the same time facies as well.

In the Sulcoretepora layer the dominant Chonetes cf. lineatus drop significantly in relative and absolute abundance (see Appendix 6.3) -- from an adjusted abundance of 66.7% in the adjoining layer beneath to 34.1% in the Sulcoretepora layer before recovering to 55.7% in the adjoining layer above. Chonetes are relatively abundant, often in reasonably good condition, and are thus readily found and measured. Might there be (and, could one predict) a change in turnover rates for Chonetes and consider that change as one of the various reactions of this assemblage to numerous other changes as an analysis of raw population counts in Appendix 6.3 shows?

The answer might be found by modeling a community interaction matrix and digraph which, when parameter change analysis is undertaken, will show changes in abundance (at least at the level of sign changes) as actually observed in the sample. The digraph and direction of abundance changes can be evaluated in order to predict the change, if any, in the turnover rate of Chonetes. Then, by measuring the size of individual Chonetes we can determine to what degree the prediction was correct. This is based on the assumption that the change in age structure (turnover rate) within the Chonetes population will be indicated in the fossil record by a change in average size. (See below for the relationship of this effort to life history theory.)

Modeling an apparent interaction matrix which leads to the correct designation of observed changes in field data population counts lends some confidence that the model constructed has some relationship to the "real" community interaction matrix. I am not seeking to elucidate the numerous and complex interactions that actually existed in a particular paleocommunity. Rather, I am attempting to see if a carefully constructed model based upon apparent interactions can be used to make a correct prediction of hierarchically related phenomena.

The following should be taken as a pilot study for two reasons. Firstly, the *Chonetes* species studied is probably *Chonetes cf. lineatus* (*Chonetes vicinus* -- Linsley in Rollins, Eldredge and Linsley, 1972), generally thought, as assumed in this study, to be one species. However, it is possible (Howard Feldman, personal communication) that there may be more than one species involved. The relatively rare larger specimens may be of a different species from the more abundant small and mid-size type. While such a possibility would have little, if any, effect on the analyses undertaken in Chapters 4 and 5, it could be quite important in the present discussion which hinges on a size change prediction. Secondly, it is not possible, certainly not in the field, to differentiate amongst the very smallest chonetids. The vast majority of these small fossils are, in these samples, probably *Chonetes cf. lineatus*; but to assume that all are would be inappropriate.

A definitive test of turnover rate predictions would require a consideration of both issues and the use of appropriate methodologies to overcome whatever potential obstacles they represent.

Parameter Changes in Hamilton Sampling Units

It is possible to construct various digraphs in such a way that when one of the entities is subjected to a parameter effect, the proper sign changes for the alterations in abundance of all the entities will be generated. However, has one generated the biologically most suitable digraph or digraphs?

A four entity system may be constructed in any of 4.3×10^{7} different ways, a five entity system in 8.5×10^{11} and a six entity system in 1.5×10^{17}, etc. From these totals must be subtracted the numerous constructions that do not meet the minimal criterion that no entity or entities should be unconnected to the remaining system. In addition, most of the remaining possible systems are patently unfeasible biologically. Nevertheless, too many possibilities remain for a systematic search.

Figure 6.1 is a digraph which, under various parameter change effects (such as a negative effect entering the system through Chonetes), indicates the observed changes in sign for the most abundant populations of the sampling units discussed. I constructed but rejected several other digraphs with correct sign changes because they were less biologically feasible than the digraph presented here.

I have selected the digraph shown in Figure 6.1 because appropriate parameter changes applied to it generate the correct sign changes for the situations both leading up to and away from the *Sulcoretepora* layer. Significantly, the latter set of sign changes is not simply the inverse of the former (see Table 6.1); the situation itself and its modeling are more complex. Further, a parameter change entering the system through *Chonetes* generates the initial changes including the decline in *Chonetes* and the increase in *Sulcoretepora*. Another parameter change entering through the *Sulcoretepora* generates the subsequent set of changes including the decrease in *Sulcoretepora* and the increase in *Chonetes*. One could use different digraphs for each of the before and after situations; but, because my data source is the fossil record and because there has been no loss of the abundant fossil populations or indications of a change in their ecological characteristics, I chose to use one digraph for both the before and after situations.

The above needs to be placed in context. I find it interesting, but *not* necessary, that parameter changes entering the system through the populations important because of their relative abundances give the expected results. However, less *apparently* important populations turn out to be potentially the locus of parameter change as well. The single population locus of parameter change may itself be more apparent than real. (In the previous Chapter, Cyrtina, a relatively unimportant population with respect to abundance, was suggested to play an important structural role in its community type.) In addition, relying upon one digraph for the before and after situation represents an appeal to parsimony as there is no indication of a need to add further complexity (see below).

The possible parameter changes and the resultant sign changes for numbers are given in Table 6.2. The formula evaluating the sign of the effect of a parameter change is given and explained in Appendix 6.5.

The assumption that one can evaluate external or internal effects on a community by means of a single parameter change entering a community through one entity is the equivalent of the argument for the applicability of Liebig's law of the minimum where the factor closest to the critical minimum is considered to be the limiting one. In addition, since the digraph and comparable community matrix represent apparent interactions, the parameter change is that perturbation upon the apparent interaction matrix which generates the already observed sign changes.

Chonetes Turnover Rates in Hamilton Sampling Units

Table 6.2 is a list of the parameter change results for Figure 6.1. Four of the five parameter changes that produce the sign results for the "before" Sulcoretepora situation can be interpreted as suggesting a possible turnover rate decrease (or average size increase) for Chonetes. The situation in which the parameter change enters the system through Chonetes is included in this group. The suggestion of a possible turnover rate decrease for Chonetes is based upon the following:

- the resource base (some combination of spatial and nutritional factors) for Chonetes increases
- the "predator" on Chonetes, low attached brachiopods, and Sulcoretepora decreases
- the low attached brachiopods, crinoids, and Sulcoretepora increase, in conformance with the field observation
- Chonetes decreases, in conformance with the field observation

It seems reasonable to predict that, with more resources for Chonetes, with fewer predators which have more alternative prey, and with fewer Chonetes, there will be a decrease in the turnover rate for Chonetes. I would predict an age structure shift to an overall older population, and, that in the fossil record, we should find the average Chonetes in the Sulcoretepora layer is larger than the average Chonetes in the older layer below.

In terms of life history tactics, this prediction can be evaluated within the context of the bet-hedging model of Schaffer (1974). He argues that in variable environments where reproductive success is diminished, reproductive effort will be decreased and there will be a longer life-span. This bet-hedging model seemingly contrasts with the r- and K-selection model (Stearns, 1976) which would lead me to postulate that the observed change in *Chonetes* characteristics represent a K-selecting environment -- that is, one that is more predictable or constant for the adults. Since it is precisely the *Sulcoretepora* layer that is most unique in the complete *Chonetes-Ambocoelia* community type sampling regime, this is difficult to accept and, at least for me, leaves open the relationship of the bet-hedging and r- and K-selection models. (See below for further discussion on life history tactics.)

Table 6.2 shows two congruent parameter change results for the "after" *Sulcoretepora* situation. Both can be interpreted to suggest a possible turnover rate increase (or average size decrease) for *Chonetes*. The results include the situation in which the parameter change enters the system through *Sulcoretepora*. However, in neither case is the analysis *as clear* as the before *Sulcoretepora* situation. The suggestion of a turnover rate increase for *Chonetes* is based upon the following:

- the resource base for *Chonetes* decreases (or, is being otherwise utilized)
- it is unclear as to the change for the "predator" on *Chonetes*, low attached brachiopods, and *Sulcoretepora* and it is possible that it may decrease

- *Chonetes* increases, in conformance with the field observation
- *Sulcoretepora* and crinoids decrease, in conformance with the field observation
- the change for low attached brachiopods is not clear but it may very well be an increase which fits the field observation

With fewer resources, perhaps fewer predators with perhaps no change in alternative prey, and more *Chonetes* I would expect an increase in turnover rate for *Chonetes*. I would predict an age structure shift to an overall younger population and, in the fossil record, we should find that the average *Chonetes* in the more recent layer above the *Sulcoretepora* layer is smaller than the average *Chonetes* in the *Sulcoretepora* layer. *This prediction is, however, somewhat tenuous.*

This prediction, in the context of life history tactics based upon a bet-hedging model, would indicate either a continuing variable environment with a change to variable adult mortality, or, a continuing reproductive success variability with a change to a more stable juvenile environment. The former, but not the latter, situation would fit the r- and K-selection model (Stearns, 1976) where the observed changes in *Chonetes* would represent an r-selecting environment. However, the after *Sulcoretepora* layer is essentially indistinguishable from all other sampling elements other than the *Sulcoretepora* layer --

again leaving open the question as to the relationship between the bet-hedging and the r- and K-selection models.

Both this and the previous life history tactics discussion need to be placed in a paleoecological context. Although the Hamilton is known to be a time of relative environmental stability (see Chapter 1), there is no precise information on degree of environmental fluctuations affecting the Chonetes-Ambocoelia community type. In addition, even with this information, it would be difficult to evaluate its effects at the existing time-space bound individual community perspective. Ascertaining variability, as required by the bet-hedging model, in reproductive success and adult mortality would be very difficult in the fossil record. Evaluating life history tactics themselves from the fossil record is essentially inappropriate.

I tested the following predictions with respect to relative average size of Chonetes:

below Sulcoretepora layer	Sulcoretepora layer	above Sulcoretepora layer
smaller	larger	smaller

Table 6.3 shows the analysis of 403 Chonetes measured as listed in Appendix 6.6. The one-tailed p-value for the t-test for the below Sulcoretepora layer and Sulcoretepora

layer measures is $p < 0.09$. The p-value for the above *Sulcoretepora* layer and *Sulcoretepora* layer measures is $p < 0.43$. The predicted trends, though not statistically significant, held with respect to the first prediction at each of the three quarry sites, and with respect to the second prediction for two of the three quarry sites.

Discussion

Two predictions were made: an increase in the average size of *Chonetes* found in the *Sulcoretepora* layer compared to the immediately preceding layer and a decrease in the average size of *Chonetes* found in the subsequent layer to the *Sulcoretepora* layer. Originally, the second prediction was a tentative one (see above). This was born out by the results. The neoecological method used indicated that the situation was not as clear-cut for the second prediction as for the first prediction. Within the hierarchical context of the method used, variable local environmental and biotic phenomena were obscured (partially indicated in that the relative abundance of *Chonetes* did not *fully* recover from the before *Sulcoretepora* layer to the after layer situation -- 66.7% to 34.1% to 55.7%). Of course, each locality presents us with a record of a series of local-ecosystems subject to their unique histories as their own particular entities. The turnover rate method, as used here, ignored this uniqueness in favor of assumed important environmental and biotic commonalities as suggested by the fossil record itself. Chapter 4 established the degree of the commonality of the _Chonetes-Ambocoelia_ community type. (Chapter 5 used this commonality as a basis for establishing the existence of structure at the community level -- again with use of another neoecological method.)

Using the turnover rate method in a parsimonious manner (i.e., just the one digraph for the before and after situations) emphasized the commonality of the fossil layers comprising the community type. The predictions, including the relative tentativeness of the second prediction, were supported (even if not definitively so) by the results.

Using the $p < 0.05$ criterion, I cannot reject a null hypothesis that there is no difference between the sets of measurements for each of the two test situations. However, the results are sufficiently suggestive that two points can be made.

Firstly, a more complete test should be undertaken in the future. Each of the nine sampling units involved should include a sufficiently large number of _Chonetes_. In the tests undertaken here, the numbers of _Chonetes_ ranged from 20 to 90 and averaged 45. Perhaps there should be at least 100 in each sampling unit. This would be about the number required to give a $p < 0.10$ at most localities (especially for the first prediction) _if_ the relative body size differences seen in the sampling regime used here were to be maintained. This maintenance of average body size differences as sample size increases is an assumption (or hope) but one has to start somewhere in planning a sampling regime. The preliminary study reported here indicates that the predictions may be valid and also show that the sample size must be increased in order to provide a more definitive answer. It would be worthwhile (see below) to determine whether or not a more definitive answer can be attained.

A larger sample size should also allow for greater comprehension of local-ecosystem effects for each of the three quarries. For instance, in looking at Appendix 6.4, it is seen that the Deep Spring Road quarry has by far the most variable fossil scoring of abundance changes for any of the three quarries. From Table 6.3, it is also seen that it is the Deep Spring Road quarry *Chonetes* that least follow the Turnover Rate predictions for both the before and after situations. There may be local-ecosystem effects at Deep Spring Road that override the broader community type effects that are being modeled here.

The second point can be elaborated through a brief statement about the significance of a test of this type. My field observations noted a significant change in the numbers of the most abundant populations from the older sampling level to the adjoining *Sulcoretepora* layer. Another set of significant changes (not solely the reverse of the first) was noted from the *Sulcoretepora* layer to the adjoining more recent level. I wished to test the possibility that these individual population changes within each layer were not independent of one another and of the community context within which they were embedded. A possible approach would be to attempt to correctly predict some phenomena based on a model of the interactions of the populations. The object of this study was to test the prediction that a physical and/or biotic environmental change would affect the relationships that constitute a community in such a way that the age structure of the Chonetes population would shift to an older average age along with the initial change in population abundances noted above and then to a younger average age along with the subsequent change in population abundances noted above. Thus, the average size of the members of the Chonetes population should be larger and then smaller in subsequent layers. My results are supportive, although not definitively so, of these predictions.

The above can be placed in Salthe's (1984) triadic hierarchical context (see Chapter 3):

upper level - the "apparent" community matrix of relationships

focal level - the observed changes in population numbers

lower level - the observed average size change in organisms of a particular population

A biotic and/or physical parameter change is "observed" to enter the community through a population. The boundary conditions imposed by the community relationships contextualize the particular changes in population numbers. These changes in population numbers have a downward cascading "effect" on organisms generating longevity or increased reproductive success. The lower level organism change then serves as the initiating conditions for an age structure change in the population. The age structure change has, within the boundaries of the community relationships, both immediate ecological and potential evolutionary implications for this and the other populations in the community.

The approach discussed in this chapter is useful in establishing the empirical usefulness of a hierarchical view as well as the validity of using neoecological tools in paleoecology. Given current views expressed within the sciences, it is fair to assume that results testing predictions embedded in a hierarchical context should be both supportive and definitive for these predictions. With such results the reality of communities (as science understands reality) would be established. We will never know the complete make-up and interactions of the component populations of communities from either paleoecological or neoecological studies. Certainly these populations and their interactions may not be identical to their respective "apparent" communities. Nevertheless, we would recognize the reality of a given community as a consequence of the rich trail of "effects" (including predictable ones) imposed by their boundary conditions.

TABLE 1.1

Major Taxa Found in the Hamilton Group

- Phylum Cnidaria
  - Class Anthozoa
    - Subclass Zooantheria (corals)
      - Order Rugosa
        - Tabulata
- Phylum Bryozoa
  - Class Stenolaemata
    - Order Cyclostomata
      - Trepostomata
      - Cryptostomata
  - Class Gymnolaemata
    - Order Ctenostomata
- Phylum Brachiopoda
  - Class Inarticulata
    - Order Lingulida
      - Acrotretida
  - Class Articulata
    - Order Orthida
      - Strophomenida
      - Pentamerida
      - Rhynchonellida
      - Spiriferida
      - Terebratulida
- Phylum Mollusca
  - Class Monoplacophora
  - Class Bivalvia
    - Subclass Paleotaxodonta
      - Order Nuculoidea
    - Subclass Cryptodonta
      - Order Praecardioda
- Phylum Mollusca (cont.)
    - Subclass Pteriomorphia
      - Order Pterioida
    - Subclass Paleoheterodonta
      - Order Modiomorpha
    - Subclass Heterodonta
      - Order Veneroida
    - Subclass Anomalodesmata
      - Order Pholadomyoida
    - Subclass uncertain
      - Order Conocardioda
  - Class Gastropoda
      - Order Archaeogastropoda
        - Caenogastropoda (Cox)
    - Class Cephalopoda
    - Subclass Nautiloidea
      - Order Orthochoanites
        - Cyrtochoanites
    - Subclass Ammonoidea
      - Order Extrasiphonata
- ?Phylum Arthropoda
  - Subphylum Crustacea
    - Class Archaeostraca
      - Ostracoda
      - Cirripedia
  - Subphylum Chelicerata
    - Class Merostomata
  - Subphylum Trilobitomorpha
    - Class Trilobita
      - Order Phacopida
- Phylum Echinodermata
  - Subphylum Crinozoa
    - Class Crinoidea

TABLE 1.2

Localities and Sampling Unit Descriptions

Ludlowville-Ledyard

a) From McCollum, 1980 - Appendix 1; collection covers lower two-thirds of Ludlowville. "The base of the section is covered by a lake and gravels eastward from the town of Blossum for approximately three-quarters of a mile." The 58 sampling units cover 23 meters in 1/2 meter intervals with separate sampling of bedding planes. Sampling goes from the oldest to the youngest rock.

Sampling Units 1-30

These Alden Member sampling units start at "Buffalo Creek opposite a prominent bluff and continue to the first major northward-flowing drainage, ... east of Windspar Road."

Sampling Units 31-58

These Elma Member sampling units start at "the mouth of 'Caughels Creek' and end at the *Pleurodictyum* beds near the junction of Bullis Road."

b) From Brett, field notes. Located near Darien Center in the State Park. The 11 sampling units cover 118 centimeters in approximately equal intervals. Sampling goes from oldest to youngest rock.

Sampling Units 59-69

These Alden Member sampling units are found in a bank of Eleven Mile Creek and start about 1.1 meters below a concretion layer and about 3.5 meters above the Centerfield limestone edge.

Moscow-Windom

a) From Pilette, field notes. Located in the Chenango Valley at four farmer's quarries. The 28 sampling units are taken in 10 centimeter intervals with the top sampling unit in each quarry being a bedding plane. Sampling goes from youngest to oldest rock.

In each of the four quarries the sampling starts at the same bedding plane. In Bradley Brook, Geer Road and Lebanon Center Road the bedding plane is approximately 6 meters above a prominent phosphate nodule bed. In Bradley Brook and Lebanon Center Road the bedding plane is approximately 2 meters below a thin calcareous fossil layer. Figure 4.1 and accompanying discussion indicate why these bedding planes are considered the same.

Sampling Units 70,71 Bradley Brook

Take Bradley Brook Road from Pierceville for 2.2 miles to Soule Road; turn right and quarry is on the left 200 feet from the turn.

Sampling Units 72, 73 and 85-91 Geer Road

Take Bradley Brook Road from Pierceville for 3.0 miles to Geer Road; turn left and continue 0.7 miles to chain across side road on left; quarry is 400 feet down the side road.

Sampling Units 74,75 and 92-97 Lebanon Center Road

Take Lebanon Road east from Lebanon for 2.5 miles and turn left on Rodman Road; continue 0.4 miles and turn left on Lebanon Center Road; continue 0.5 miles to outcrop dropping down from right side of road.

Sampling Units 76,77 and 78-84 Deep Spring Road

Take Lebanon Road east from Lebanon for 1.0 mile and turn right on Deep Spring Road; continue 1.2 miles to quarry on right side of road.

b) From Brett, field notes. Located behind WKBW tower in the woods. The 10 sampling units cover 120 centimeters in approximately equal intervals. Sampling goes from oldest to youngest rocks.

Sampling Units 98-107

These start at KB Creek 1.25 meters above a concretion bed which is just above a calcareous bed near stream level.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		1	2	3	4	5	6	7	8	9
1.	"Lingula"	11	7	10	3	1			4	1
2.	Craniops hamiltoniae		6	2						
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media	8	16							
5.	Orthostrophia strophomen.									
6.	Rhipidomella vanuxemi									
7.	"Tropidoleptus"									
8.	Protoleptostrophia perplana									
9.	Megastrophia concava									
10.	Strophonella ampla									
11.	Schuchertella arctostriatus	1								
12.	Devonochonetes setigerus	10	7	13	12	17	37		1	53
13.	Devonochonetes scitulus									
14.	Devonochonetes coronatus									
15.	Longispina mucronatus	33	27	18						
16.	Chonetes cf. lineatus									
17.	Truncalosia truncata									
18.	Productella									
19.	Spinulicosta spinulicosta									
20.	Camarotoechia congregata									
21.	"Leiorynchus" sp.	19	56		28	31	229	12	103	176
22.	Atrypa									
23.	Athyris spiriferoides									
24.	Ambocoelia umbonata	7	9	11	6	9	16			3
25.	Pustulatia									
26.	Cyrtina hamiltonensis									
27.	Megakoslowskiella sulcata									
28.	Mucrospirifer mucronatus		2			2				
29.	Mucrospirifer consobrinus									
30.	"Tylothyris"									
31.	Spinocyrtia granulosa									
32.	Mediospirifer									
33.	Elita fimbriata									
34.	"Rhipidothyris"									
35.	Tellinopsis subemarginata									
36.	Nucula bellistriata									
37.	Nucula corbuliformis									
38.	Nucula lirata									
39.	Nucula opima									
40.	Nuculites oblongatus									
41.	Nuculites triqueter									
42.	Nuculites sp.									
43.	Palaeoneilo constricta									
44.	Palaeoneilo fecunda									

	Sampling Unit								
	1	2	3	4	5	6	7	8	9
45. Palaeoneilo halli									
46. Palaeoneilo marginata									
47. Palaeoneilo sp.									
48. Nuculana									
49. nuculoidea/nuculites	2						178		29
50. Praecardium potens									
51. Buchiola retrostriata									
52. Pararca									
53. Lunulacardium curtum									
54. Pterchaenia fragilis	6	3	4		3	5		1	2
55. Mytilarca									
56. Leptodesma conradi					1				
57. Leiopteria									
58. Ptychopteria boydi									
59. Actinopteria boydi									
60. Nyassa									
61. Pterinopecten									
62. Pseudoaviculopecten									
63. Lyriopecten									
64. Aviculopecten									
65. pectinids									
66. Modiomorpha concentrica									
67. Modiomorpha mytiloides									
68. Modiomorpha subalata							4		
69. Goniophora pygmaea									
70. Modiella pygmaea									
71. Cypricardella bellistriata?									
72. Cypricardinia indenta									
73. Grammysia									
74. Grammysioidea alveata									
75. Glossites									
76. Parallelodon hamiltoniae									
77. Solemya vetusta									
78. bryozoans sp. 1									
79. bryozoans sp. 2									
80. Eliasopora stellata									
81. Reptaria									
82. cyclostomate									
83. Eridotrypella obliqua									
84. trepostomate									
85. Loculipora									
86. Polypora incepta									
87. Unitrypa scalaris									
88. Sulcoretepora gilberti									

	Sampling Unit 1	2	3	4	5	6	7	8	9
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2									
92. gastropods 1									
93. gastropods 2									
94. "Cyrtolites"									
95. "Bucania"									
96. Retispira leda									
97. Patellilabia lyra									
98. bellerophontid									
99. Straparollus laxus									
100. Mourlonia itys									
101. Mourlonia lucina									
102. Glyptomaria capillaria		1	2						
103. Gyroma									
104. Holopea									
105. Naticonema									
106. Platyceras					1				
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.	11	11						2	2
110. Dechenella									
111. Phacops rana					1	1			
112. Greenops boothi	2	4			2	3			1
113. crinoids		p							
114. Michelinoceras				p	p				p
115. Striacoceras									
116. Spyroceras		p							
117. Bactrites									
118. Tornoceras								p	p
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum									
123. Cladochonus dichotoma	p	p							
124. auloporids									
125. hyolithids									
126. Styliolina fissurella	p	p	p	p	p	p		p	p
127. Tentaculites	p	p	p	p	p	p			p
128. Coleolus									
129. Cornulites									
130. ostracodes									
131. Ponderodictya punctulifera	p	p	p	p	p	p		p	p
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		10	11	12	13	14	15	16	17	18
1.	"Lingula"									
2.	Craniops hamiltoniae						3	4		
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media									
5.	Orthostrophia strophomen.									
6.	Rhipidomella									
7.	Tropidoleptus									
8.	Protoleptostrophia									
9.	Megastrophia concava									
10.	Strophonella ampla									
11.	Schuchertella				9	1	6	4		
12.	Devonochonetes setigerus	84	91	93	126	224	303	316	9	400
13.	Devonochonetes scitulus									
14.	Devonochonetes coronatus									
15.	Longispina								3	
16.	Chonetes cf. lineatus									
17.	Truncalosia truncata									
18.	Productella									
19.	Spinulicosta spinulicosta									
20.	Camarotoecia congregata				27			23		76
21.	"Leiorynchus" sp.	116	138	161	203	252	461	382		560
22.	Atrypa									
23.	Athyris spiriferoides									
24.	Ambocoelia umbonata	16	24		71	170	141	21		47
25.	Pustulatia									
26.	Cyrtina									
27.	Delthyris sulcata									
28.	Mucrospirifer mucronatus							16		
29.	Mucrospirifer consobrinus									
30.	Tylothyris mesocostalis									
31.	Spinocyrtia granulosa			1		3	2			
32.	Mediospirifer									
33.	Elytha fimbriata									
34.	Rhipidothyris lepida									
35.	Tellinopsis									
36.	Nucula bellistriata									
37.	Nucula corbuliformis									
38.	Nucula lirata									
39.	Nucula opima									
40.	Nuculites oblongatus									
41.	Nuculites triqueter									
42.	Nuculites sp.									
43.	Palaeoneilo constricta									
44.	Palaeoneilo fecunda									

		Sampling Unit								
		10	11	12	13	14	15	16	17	18
45.	Palaeoneilo halli					1				
46.	Palaeoneilo marginata									
47.	Palaeoneilo sp.									
48.	Nuculana									
49.	nuculoidea/nuculites	2		1		1	2		222	
50.	Praecardium									
51.	Buciola									
52.	Pararca									
53.	Lunulacardium curtum									
54.	Pteriochaenia	5	9	3		4	12	3		5
55.	Mytilarca									
56.	Leptodesma									
57.	Leiopteria									
58.	Ptychopteria boydi									
59.	Actinopteria boydi									
60.	Nyassa									
61.	Pterinopectin									
62.	Pseudoaviculopectin									
63.	Lyriopectin									
64.	Aviculopectin									
65.	pectinids									
66.	Modiomorpha concentrica									
67.	Modiomorpha mytiloides									
68.	Modiomorpha subalata					3	4			3
69.	Goniophora pygmaea								2	
70.	Modiella									
71.	Cypricardella bellistriata?						3			
72.	Cypricardinia									
73.	Grammysia									
74.	Grammysioidea									
75.	Glossites									
76.	Parallelodon									
77.	Solemya									
78.	bryozoans sp. 1						2			
79.	bryozoans sp. 2									
80.	Eliasopora stellata									
81.	Reptaria									
82.	cyclostomate									
83.	Eridotrypella obliqua									
84.	trepostomate									
85.	Loculipora									
86.	Polypora incepta									
87.	Unitrypa									
88.	Sulcoretepora gilberti									

	Sampling Unit								
	10	11	12	13	14	15	16	17	18
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2									
92. gastropods 1									
93. gastropods 2									
94. Cyrtolites									
95. "Bucania"									
96. Retispira leda	4	5		3			1		
97. Patellilabia lyra									
98. bellerophontid									
99. Straparollus laxus									
100. Mourlonia itys									
101. Mourlonia lucina									
102. Glyptomaria capillaria									
103. Gyroma									
104. Holopea							1		
105. Naticonema									
106. Platyceras		1							
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.			2		2		5		8
110. Dechenella									
111. Phacops rana	4	7		4	10	4	6		9
112. Greenops boothi		3		5	13	5	9		14
113. crinoids						p			p
114. Michelinoceras					p		p		
115. Striacoceras									
116. Spyroceras									
117. Bactrites									
118. Tornoceras	p								
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum		p							
123. Cladochonus dichotoma			p		p	p	p		p
124. auloporids									
125. hyolithids									
126. Styliolina fissurella	p	p	p	p	p	p	p		p
127. Tentaculites	p	p	p	p	p	p	p		p
128. Coleolus									
129. Cornulites									
130. ostracodes									
131. Ponderodictya punctulifera	p	p	p	p	p	p	p		p
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		19	20	21	22	23	24	25	26	27
1.	"Lingula"									
2.	Craniops hamiltoniae									
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media									
5.	Orthostrophia strophomen.									
6.	Rhipidomella									
7.	Tropidoleptus									
8.	Protoleptostrophia									
9.	Megastrophia concava									
10.	Strophonella ampla									
11.	Schuchertella									
12.	Devonochonetes setigerus	385	371	181	171		137	137	150	170
13.	Devonochonetes scitulus									
14.	Devonochonetes coronatus									
15.	Longispina				12		9			
16.	Chonetes cf. lineatus									
17.	Truncalosia truncata			11						
18.	Productella									
19.	Spinulicosta spinulicosta									
20.	Camarotoecia congregata			44				12	21	30
21.	"Leiorynchus" sp.	412	546	397	213	41	205	180	125	150
22.	Atrypa									
23.	Athyris spiriferoides									
24.	Ambocoelia umbonata		42	29	39		43	25	18	
25.	Pustulatia									
26.	Cyrtina									
27.	Delthyris sulcata									
28.	Mucrospirifer mucronatus			38	31		27	16	20	
29.	Mucrospirifer consobrinus									
30.	Tylothyris mesocostalis									
31.	Spinocyrtia granulosa									
32.	Mediospirifer									
33.	Elytha fimbriata									
34.	Rhipidothyris lepida									
35.	Tellinopsis									
36.	Nucula bellistriata									
37.	Nucula corbuliformis									
38.	Nucula lirata									
39.	Nucula opima									
40.	Nuculites oblongatus		3							
41.	Nuculites triqueter									
42.	Nuculites sp.									
43.	Palaeoneilo constricta									
44.	Palaeoneilo fecunda									

		Sampling Unit								
		19	20	21	22	23	24	25	26	27
45.	Palaeoneilo halli									1
46.	Palaeoneilo marginata									
47.	Palaeoneilo sp.									
48.	Nuculana									
49.	nuculoidea/nuculites					316			2	1
50.	Praecardium									
51.	Buciola									
52.	Pararca									
53.	Lunulacardium curtum	3								
54.	Pteriochaenia				3		7	4	8	17
55.	Mytilarca									
56.	Leptodesma									2
57.	Leiopteria									
58.	Ptychopteria boydi									
59.	Actinopteria boydi									
60.	Nyassa									
61.	Pterinopectin									
62.	Pseudoaviculopectin									
63.	Lyriopectin									
64.	Aviculopectin									
65.	pectinids									
66.	Modiomorpha concentrica									
67.	Modiomorpha mytiloides									
68.	Modiomorpha subalata									
69.	Goniophora pygmaea									
70.	Modiella									
71.	Cypricardella bellistriata?									
72.	Cypricardinia									
73.	Grammysia									
74.	Grammysioidea									
75.	Glossites									
76.	Parallelodon									
77.	Solemya									
78.	bryozoans sp. 1									
79.	bryozoans sp. 2									
80.	Eliasopora stellata									
81.	Reptaria									
82.	cyclostomate									
83.	Eridotrypella obliqua									
84.	trepostomate									
85.	Loculipora									
86.	Polypora incepta									
87.	Unitrypa									
88.	Sulcoretepora gilberti									

	Sampling Unit								
	19	20	21	22	23	24	25	26	27
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2									
92. gastropods 1				59					
93. gastropods 2									
94. Cyrtolites									
95. "Bucania"									
96. Retispira leda			4	4		5		3	3
97. Patellilabia lyra									
98. bellerophontid									
99. Straparollus laxus									
100. Mourlonia itys									
101. Mourlonia lucina									
102. Glyptomaria capillaria									
103. Gyroma									
104. Holopea									
105. Naticonema	41								
106. Platyceras									
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.									
110. Dechenella									
111. Phacops rana			1			3			
112. Greenops boothi			6	2		4	2		
113. crinoids	p		p						
114. Michelinoceras		p		p			p	p	p
115. Striacoceras									
116. Spyroceras									
117. Bactrites									
118. Tornoceras				p			p		
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum									
123. Cladochonus dichotoma	p	p				p			
124. auloporids									
125. hyolithids									
126. Styliolina fissurella	p	p	p	p		p	p	p	p
127. Tentaculites	p	p	p	p		p	p	p	p
128. Coleolus									
129. Cornulites									
130. ostracodes						p			p
131. Ponderodictya punctulifera	p	p	p	p		p	p	p	p
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		28	29	30	31	32	33	34	35	36
1.	"Lingula"									
2.	Craniops hamiltoniae									
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media									
5.	Orthostrophia strophomen.									
6.	Rhipidomella vanuxemi									
7.	"Tropidoleptus"									
8.	Protoleptostrophia perplana									
9.	Megastrophia concava									
10.	Strophonella ampla									
11.	Schuchertella arctostriatus		14							
12.	Devonochonetes setigerus	125	310	5	122	240	130		72	130
13.	Devonochonetes scitulus									
14.	Devonochonetes coronatus									
15.	Longispina mucronatus		67		1					
16.	Chonetes cf. lineatus									
17.	Truncalosia truncata		34			70				
18.	Productella									
19.	Spinulicosta spinulicosta									
20.	Camarotoechia congregata	17	70							
21.	"Leiorynchus" sp.	280	350						21	
22.	Atrypa									
23.	Athyris spiriferoides									
24.	Ambocoelia umbonata		155	4	38	27	22		32	48
25.	Pustulatia									
26.	Cyrtina hamiltonensis									
27.	Megakoslowskiella sulcata									
28.	Mucrospirifer mucronatus		130		16	33	46			40
29.	Mucrospirifer consobrinus									
30.	"Tylothyris"									
31.	Spinocyrtia granulosa		4							
32.	Mediospirifer									
33.	Elita fimbriata									
34.	"Rhipidothyris"					180				
35.	Tellinopsis subemarginata			6						
36.	Nucula bellistriata									
37.	Nucula corbuliformis									
38.	Nucula lirata									
39.	Nucula opima									
40.	Nuculites oblongatus			16						
41.	Nuculites triqueter									
42.	Nuculites sp.									
43.	Palaeoneilo constricta			10						
44.	Palaeoneilo fecunda									

		Sampling Unit								
		28	29	30	31	32	33	34	35	36
45.	Palaeoneilo halli									
46.	Palaeoneilo marginata									
47.	Palaeoneilo sp.									
48.	Nuculana									
49.	nuculoidea/nuculites		16	58		10		187		
50.	Praecardium potens			4		1				
51.	Buchiola retrostriata									
52.	Pararca									
53.	Lunulacardium curtum									
54.	Pterchaenia fragilis	4		1	8	16	20		9	3
55.	Mytilarca									
56.	Leptodesma conradi									
57.	Leiopteria									
58.	Ptychopteria boydi		3		1	1				
59.	Actinopteria boydi									
60.	Nyassa									
61.	Pterinopecten									
62.	Pseudoaviculopecten									
63.	Lyriopecten									
64.	Aviculopecten									
65.	pectinids									
66.	Modiomorpha concentrica									
67.	Modiomorpha mytiloides									
68.	Modiomorpha subalata		8		6					2
69.	Goniophora pygmaea									
70.	Modiella pygmaea									
71.	Cypricardella bellistriata?									
72.	Cypricardinia indenta									
73.	Grammysia									
74.	Grammysioidea alveata			3						
75.	Glossites									
76.	Parallelodon hamiltoniae									
77.	Solemya vetusta									
78.	bryozoans sp. 1									
79.	bryozoans sp. 2									
80.	Eliasopora stellata									
81.	Reptaria									
82.	cyclostomate		3				16			
83.	Eridotrypella obliqua									
84.	trepostomate									
85.	Loculipora									
86.	Polypora incepta									
87.	Unitrypa scalaris									
88.	Sulcoretepora gilberti									

	Sampling Unit								
	28	29	30	31	32	33	34	35	36
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2									
92. gastropods 1									
93. gastropods 2									
94. "Cyrtolites"									
95. "Bucania"									
96. Retispira leda	3		2		5	10			11
97. Patellilabia lyra									
98. bellerophontid									
99. Straparollus laxus		3	14				5	3	
100. Mourlonia itys									
101. Mourlonia lucina									
102. Glyptomaria capillaria									
103. Gyroma									
104. Holopea									
105. Naticonema									
106. Platyceras		13							
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.		15							
110. Dechenella									
111. Phacops rana		11			3	3			
112. Greenops boothi		5			1	5			
113. crinoids		p		p				p	p
114. Michelinoceras	p		p		p	p			
115. Striacoceras									
116. Spyroceras									
117. Bactrites									
118. Tornoceras					p				
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum									
123. Cladochonus dichotoma		p							
124. auloporids									
125. hyolithids									
126. Styliolina fissurella	p	p	p	p	p	p		p	p
127. Tentaculites	p	p	p		p			p	
128. Coleolus									
129. Cornulites									
130. ostracodes			p	p	p	p		p	p
131. Ponderodictya punctulifera	p	p	p	p	p	p		p	p
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		37	38	39	40	41	42	43	44	45
1.	"Lingula"									
2.	Craniops hamiltoniae									
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media				5					
5.	Orthostrophia strophomen.									
6.	Rhipidomella									
7.	Tropidoleptus			16						2
8.	Protoleptostrophia									
9.	Megastrophia concava									
10.	Strophonella ampla									
11.	Schuchertella			20	22					3
12.	Devonochonetes setigerus	168	122	210	325	200	189	223	11	260
13.	Devonochonetes scitulus									
14.	Devonochonetes coronatus									
15.	Longispina									
16.	Chonetes cf. lineatus									
17.	Truncalosia truncata									
18.	Productella									
19.	Spinulicosta spinulicosta									
20.	Camarotoecia congregata									
21.	"Leiorynchus" sp.	32	55	43	116		17			
22.	Atrypa									
23.	Athyris spiriferoides									
24.	Ambocoelia umbonata	64	73	145	158	74	24	61	2	50
25.	Pustulatia									
26.	Cyrtina									
27.	Delthyris sulcata									
28.	Mucrospirifer mucronatus	35		27	200	78	31	54		47
29.	Mucrospirifer consobrinus									
30.	Tylothyris mesocostalis									
31.	Spinocyrtia granulosa						11			
32.	Mediospirifer									
33.	Elytha fimbriata									
34.	Rhipidothyris lepida									
35.	Tellinopsis									
36.	Nucula bellistriata									
37.	Nucula corbuliformis									
38.	Nucula lirata									
39.	Nucula opima									
40.	Nuculites oblongatus				2					
41.	Nuculites triqueter									
42.	Nuculites sp.			5						
43.	Palaeoneilo constricta									
44.	Palaeoneilo fecunda									

		Sampling Unit								
		37	38	39	40	41	42	43	44	45
45.	Palaeoneilo halli									
46.	Palaeoneilo marginata									
47.	Palaeoneilo sp.									
48.	Nuculana									
49.	nuculoidea/nuculites				2				230	2
50.	Praecardium									
51.	Buciola									
52.	Pararca									
53.	Lunulacardium curtum									
54.	Pteriochaenia	8	5	19	25	8		16		18
55.	Mytilarca									
56.	Leptodesma						7			
57.	Leiopteria									
58.	Ptychopteria boydi									
59.	Actinopteria boydi									
60.	Nyassa									
61.	Pterinopectin									
62.	Pseudoaviculopectin							1		
63.	Lyriopectin									
64.	Aviculopectin									
65.	pectinids									
66.	Modiomorpha concentrica									
67.	Modiomorpha mytiloides									
68.	Modiomorpha subalata				6				7	3
69.	Goniophora pygmaea									
70.	Modiella									
71.	Cypricardella bellistriata?		1							
72.	Cypricardinia									
73.	Grammysia									
74.	Grammysioidea									
75.	Glossites									
76.	Parallelodon									
77.	Solemya									
78.	bryozoans sp. 1									
79.	bryozoans sp. 2									
80.	Eliasopora stellata									
81.	Reptaria									
82.	cyclostomate							4		5
83.	Eridotrypella obliqua									
84.	trepostomate									
85.	Loculipora									
86.	Polypora incepta									
87.	Unitrypa									
88.	Sulcoretepora gilberti									

	Sampling Unit								
	37	38	39	40	41	42	43	44	45
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2									
92. gastropods 1									
93. gastropods 2									
94. Cyrtolites									
95. "Bucania"									
96. Retispira leda	13	4	12	18	10	6	12		11
97. Patellilabia lyra									
98. bellerophontid									
99. Straparollus laxus		2		3					
100. Mourlonia itys									
101. Mourlonia lucina									
102. Glyptomaria capillaria						10			
103. Gyroma									
104. Holopea									
105. Naticonema									
106. Platyceras									
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.									
110. Dechenella									
111. Phacops rana	3		6	8	2	3	2		
112. Greenops boothi				10	4	5	2		3
113. crinoids	p	p		p					p
114. Michelinoceras	p	p	p		p				p
115. Striacoceras									
116. Spyroceras									
117. Bactrites									
118. Tornoceras		p							
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum									
123. Cladochonus dichotoma									
124. auloporids									
125. hyolithids									
126. Styliolina fissurella	p	p	p	p	p	p	p		p
127. Tentaculites		p	p	p	p	p	p		p
128. Coleolus									
129. Cornulites									
130. ostracodes	p	p	p	p	p	p	p		p
131. Ponderodictya punctulifera	p	p	p	p	p	p	p		p
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		46	47	48	49	50	51	52	53	54
1.	"Lingula"									
2.	Craniops hamiltoniae		1							
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media		18				9		23	
5.	Orthostrophia strophomen.									
6.	Rhipidomella		19						10	3
7.	Tropidoleptus				31	300		126		461
8.	Protoleptostrophia		4						3	
9.	Megastrophia concava									
10.	Strophonella ampla									
11.	Schuchertella		23			3	2		12	4
12.	Devonochonetes setigerus	195	20	61	17	256	138	105	31	117
13.	Devonochonetes scitulus									
14.	Devonochonetes coronatus									
15.	Longispina									
16.	Chonetes cf. lineatus									
17.	Truncalosia truncata					11		207		383
18.	Productella									
19.	Spinulicosta spinulicosta									
20.	Camarotoecia congregata									1
21.	"Leiorynchus" sp.									
22.	Atrypa									
23.	Athyris spiriferoides		27						16	
24.	Ambocoelia umbonata	113	17	23	55	249		37		
25.	Pustulatia			2		10				
26.	Cyrtina									
27.	Delthyris sulcata									
28.	Mucrospirifer mucronatus	120	11	76	29	177	47	56	20	86
29.	Mucrospirifer consobrinus									
30.	Tylothyris mesocostalis									
31.	Spinocyrtia granulosa									
32.	Mediospirifer									
33.	Elytha fimbriata									
34.	Rhipidothyris lepida					300				
35.	Tellinopsis									
36.	Nucula bellistriata									
37.	Nucula corbuliformis									
38.	Nucula lirata									
39.	Nucula opima									
40.	Nuculites oblongatus		1	1						8
41.	Nuculites triqueter									
42.	Nuculites sp.						3			
43.	Palaeoneilo constricta		3							
44.	Palaeoneilo fecunda									

		Sampling Unit								
		46	47	48	49	50	51	52	53	54
45.	Palaeoneilo halli									11
46.	Palaeoneilo marginata					1			2	
47.	Palaeoneilo sp.									
48.	Nuculana									
49.	nuculoidea/nuculites		1	3				5	3	9
50.	Praecardium									
51.	Buciola									
52.	Pararca									
53.	Lunulacardium curtum									
54.	Pteriochaenia	18		4	1	19		24		12
55.	Mytilarca									
56.	Leptodesma			1		2				
57.	Leiopteria									
58.	Ptychopteria boydi					2				4
59.	Actinopteria boydi									
60.	Nyassa									
61.	Pterinopectin				4	24				1
62.	Pseudoaviculopectin				32	91				1
63.	Lyriopectin									
64.	Aviculopectin									
65.	pectinids									
66.	Modiomorpha concentrica									
67.	Modiomorpha mytiloides									
68.	Modiomorpha subalata		3	7		5			9	5
69.	Goniophora pygmaea									
70.	Modiella									
71.	Cypricardella bellistriata?									2
72.	Cypricardinia									
73.	Grammysia									
74.	Grammysioidea									
75.	Glossites									
76.	Parallelodon									
77.	Solemya									
78.	bryozoans sp. 1			1						
79.	bryozoans sp. 2									
80.	Eliasopora stellata								2	
81.	Reptaria									
82.	cyclostomate			32		10				47
83.	Eridotrypella obliqua									
84.	trepostomate									
85.	Loculipora									
86.	Polypora incepta									
87.	Unitrypa									
88.	Sulcoretepora gilberti									

	Sampling Unit 46	47	48	49	50	51	52	53	54
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2									
92. gastropods 1									
93. gastropods 2									
94. Cyrtolites									
95. "Bucania"									
96. Retispira leda	16		11		9		10		7
97. Patellilabia lyra		2							
98. bellerophontid									
99. Straparollus laxus		1							
100. Mourlonia itys									
101. Mourlonia lucina									
102. Glyptomaria capillaria									9
103. Gyroma									
104. Holopea									
105. Naticonema									
106. Platyceras								1	
107. Platystoma lineata			1		1	2			
108. "Elasmonema"		2		1	1				
109. Palaeozygopleura hamilton.		5				7	6	4	17
110. Dechenella									
111. Phacops rana	6	5	431	15	107	21	29	6	31
112. Greenops boothi	9	3	144		46		11		14
113. crinoids	p	p	p		p	p	p		p
114. Michelinoceras		p				p	p		p
115. Striacoceras									
116. Spyroceras									
117. Bactrites									
118. Tomoceras	p	p	p						
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum									
123. Cladochonus dichotoma		p			p	p	p	p	p
124. auloporids									
125. hyolithids									
126. Styliolina fissurella	p	p	p		p	p	p		
127. Tentaculites	p	p	p		p	p			
128. Coleolus									
129. Cornulites									
130. ostacodes	p	p	p		p				
131. Ponderodictya punctulifera	p	p	p		p	p	p		p
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		55	56	57	58	59	60	61	62	63
1.	"Lingula"					3	3	4	2	2
2.	Craniops hamiltoniae					31	77	9	7	70
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media	1								
5.	Orthostrophia strophomen.									
6.	Rhipidomella vanuxemi									
7.	"Tropidoleptus"	441	150	45						
8.	Protoleptostrophia perplana				7					
9.	Megastrophia concava									
10.	Strophonella ampla									
11.	Schuchertella arctostriatus	4					1		4	4
12.	Devonochonetes setigerus	125	86		79					
13.	Devonochonetes scitulus									
14.	Devonochonetes coronatus					36	1	5	2	4
15.	Longispina mucronatus					3				1
16.	Chonetes cf. lineatus									
17.	Truncalosia truncata	492	150							
18.	Productella									
19.	Spinulicosta spinulicosta									
20.	Camarotoechia congregata									
21.	"Leiorynchus" sp.									
22.	Atrypa									
23.	Athyris spiriferoides									
24.	Ambocoelia umbonata		32	100		23	22	24	85	48
25.	Pustulatia									1
26.	Cyrtina hamiltonensis							1	1	
27.	Megakoslowskiella sulcata									
28.	Mucrospirifer mucronatus	81	40	9	56	3	2	1	1	
29.	Mucrospirifer consobrinus									
30.	"Tylothyris"									
31.	Spinocyrtia granulosa							1		1
32.	Mediospirifer									
33.	Elita fimbriata									
34.	"Rhipidothyris"									
35.	Tellinopsis subemarginata		5							
36.	Nucula bellistriata									
37.	Nucula corbuliformis					5	3	5	4	3
38.	Nucula lirata									
39.	Nucula opima									
40.	Nuculites oblongatus	9						1		1
41.	Nuculites triqueter							1		
42.	Nuculites sp.									
43.	Palaeoneilo constricta						2	3	2	2
44.	Palaeoneilo fecunda					5	1	1	3	2

		Sampling Unit								
		55	56	57	58	59	60	61	62	63
45.	Palaeoneilo halli	12	2							
46.	Palaeoneilo marginata					3				
47.	Palaeoneilo sp.					3	1		2	
48.	Nuculana									
49.	nuculoidea/nuculites	11								
50.	Praecardium potens									
51.	Buchiola retrostriata	2								
52.	Pararca									
53.	Lunulacardium curtum			2						
54.	Pterchaenia fragilis		4				1	2	3	1
55.	Mytilarca									
56.	Leptodesma conradi	1								
57.	Leiopteria									
58.	Ptychopteria boydi	3	21	6						
59.	Actinopteria boydi									
60.	Nyassa									
61.	Pterinopecten			4						
62.	Pseudoaviculopecten									
63.	Lyriopecten									
64.	Aviculopecten									
65.	pectinids									1
66.	Modiomorpha concentrica									
67.	Modiomorpha mytiloides									
68.	Modiomorpha subalata	8	3							
69.	Goniophora pygmaea									
70.	Modiella pygmaea	1	8						1	1
71.	Cypricardella bellistriata?									
72.	Cypricardinia indenta									
73.	Grammysia									
74.	Grammysioidea alveata		1							
75.	Glossites									
76.	Parallelodon hamiltoniae									
77.	Solemya vetusta									
78.	bryozoans sp. 1									
79.	bryozoans sp. 2									
80.	Eliasopora stellata									
81.	Reptaria	80								
82.	cyclostomate	33	7							
83.	Eridotrypella obliqua									
84.	trepostomate								17	25
85.	Loculipora								1	
86.	Polypora incepta									
87.	Unitrypa scalaris									
88.	Sulcoretepora gilberti									

	Sampling Unit								
	55	56	57	58	59	60	61	62	63
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2									
92. gastropods 1									
93. gastropods 2									
94. "Cyrtolites"							1		
95. "Bucania"				2					
96. Retispira leda	13	11							
97. Patellilabia lyra		2							
98. bellerophontid							1		1
99. Straparollus laxus									
100. Mourlonia itys					5	2	3	5	2
101. Mourlonia lucina									
102. Glyptomaria capillaria	5	27	14						
103. Gyroma			10						
104. Holopea									
105. Naticonema									
106. Platyceras		2					1		2
107. Platystoma lineata	3	15							
108. "Elasmonema"									
109. Palaeozygopleura hamilton.	7	17			5	2	4	28	2
110. Dechenella									
111. Phacops rana	37	10			2	3	3	3	1
112. Greenops boothi	16				5	4	4	7	7
113. crinoids	p	p	p						p
114. Michelinoceras	p	p			p	p	p		p
115. Striacoceras									
116. Spyroceras								p	
117. Bactrites									
118. Tornoceras					p	p	p	p	p
119. ammonoids									
120. sponges							p		
121. Conularia		p							
122. Stereolasma rectum									
123. Cladochonus dichotoma	p								
124. auloporids								p	
125. hyolithids							p		
126. Styliolina fissurella	p	p	p			p	p	p	
127. Tentaculites									
128. Coleolus									
129. Cornulites					p				
130. ostacodes	p	p				p			
131. Ponderodictya punctulifera	p	p							
132. Cyrtonella			p						

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		64	65	66	67	68	69	70	71	72
1.	"Lingula"	5	10	8	1	3				
2.	Craniops hamiltoniae	81	117	44	10	25	5	12	6	8
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media					1		6	16	6
5.	Orthostrophia strophomen.								4	
6.	Rhipidomella								2	
7.	Tropidoleptus							7	9	75
8.	Protoleptostrophia		1			1				
9.	Megastrophia concava									
10.	Strophonella ampla								3	4
11.	Schuchertella	1	19	5						
12.	Devonochonetes setigerus									
13.	Devonochonetes scitulus								4	
14.	Devonochonetes coronatus	15	16	10	6	22	135	4	8	6
15.	Longispina	7	17	6	5	5	2			1
16.	Chonetes cf. lineatus							325	183	352
17.	Truncalosia truncata									
18.	Productella				1					
19.	Spinulicosta spinulicosta									
20.	Camarotoecia congregata									
21.	"Leiorynchus" sp.							6	3	2
22.	Atrypa			1					1	
23.	Athyris spiriferoides							1	4	
24.	Ambocoelia umbonata	98	184	91	20	35	35	76	119	73
25.	Pustulatia		2	95	58	4	2			
26.	Cyrtina							15	8	18
27.	Delthyris sulcata									
28.	Mucrospirifer mucronatus	2	1	2		7	17	1	3	3
29.	Mucrospirifer consobrinus									
30.	Tylothyris mesocostalis							4	3	11
31.	Spinocyrtia granulosa									
32.	Mediospirifer				1					
33.	Elytha fimbriata							1		
34.	Rhipidothyris lepida									
35.	Tellinopsis				1					
36.	Nucula bellistriata							2		1
37.	Nucula corbuliformis	1	3		9	6	3	3	9	3
38.	Nucula lirata								4	
39.	Nucula opima							1	1	1
40.	Nuculites oblongatus	1	1		1		1	3	5	3
41.	Nuculites triqueter								1	
42.	Nuculites sp.									
43.	Palaeoneilo constricta	8	1		1	2	1			
44.	Palaeoneilo fecunda	5	9	6	1					

		Sampling Unit								
		64	65	66	67	68	69	70	71	72
45.	Palaeoneilo halli									
46.	Palaeoneilo marginata				1	1		3		3
47.	Palaeoneilo sp.			2	1					
48.	Nuculana									
49.	nuculoidea/nuculites									
50.	Praecardium									
51.	Buciola									
52.	Pararca									
53.	Lunulacardium curtum									
54.	Pteriochaenia	3	4	1	4	8	6	2		
55.	Mytilarca									
56.	Leptodesma									
57.	Leiopteria									
58.	Ptychopteria boydi									
59.	Actinopteria boydi								1	
60.	Nyassa									
61.	Pterinopectin									
62.	Pseudoaviculopectin									
63.	Lyriopectin									
64.	Aviculopectin	1								
65.	pectinids			1						
66.	Modiomorpha concentrica									
67.	Modiomorpha mytiloides								3	
68.	Modiomorpha subalata									
69.	Goniophora pygmaea									
70.	Modiella	1		1	1	1	1			
71.	Cypricardella bellistriata?									
72.	Cypricardinia		2	1	4	1				
73.	Grammysia	1	3	1		1				
74.	Grammysioidea									
75.	Glossites									
76.	Parallelodon									
77.	Solemya									
78.	bryozoans sp. 1									
79.	bryozoans sp. 2									
80.	Eliasopora stellata									
81.	Reptaria									
82.	cyclostomate									
83.	Eridotrypella obliqua									
84.	trepostomate	43	58	55	64	37	1			
85.	Loculipora									
86.	Polypora incepta									4
87.	Unitrypa									
88.	Sulcoretepora gilberti									

	Sampling Unit								
	64	65	66	67	68	69	70	71	72
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2									1
92. gastropods 1									
93. gastropods 2									
94. Cyrtolites		1							
95. "Bucania"									
96. Retispira leda									
97. Patellilabia lyra									
98. bellerophontid	1	1			1	1			
99. Straparollus laxus									
100. Mourlonia itys	3	9	5	11	9	4			
101. Mourlonia lucina									
102. Glyptomaria capillaria							1	5	
103. Gyroma									
104. Holopea									
105. Naticonema									1
106. Platyceras									
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.	10	12	9	7	26	13			
110. Dechenella									
111. Phacops rana	1	3	9	10	13	1	2	1	2
112. Greenops boothi	2	6	12	4	7	6		1	1
113. crinoids	p	p			p		p	p	p
114. Michelinoceras	p	p	p	p	p	p		p	
115. Striacoceras									
116. Spyroceras								p	
117. Bactrites					p				
118. Tornoceras	p	p	p	p	p	p			
119. ammonoids							p		
120. sponges	p								
121. Conularia	p			p					
122. Stereolasma rectum									
123. Cladochonus dichotoma									
124. auloporids			p						
125. hyolithids									
126. Styliolina fissurella	p	p	p		p	p	p		
127. Tentaculites									
128. Coleolus									
129. Cornulites									
130. ostracodes				p	p				
131. Ponderodictya punctulifera									
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		73	74	75	76	77	78	79	80	81
1.	"Lingula"									
2.	Craniops hamiltoniae	4	1	3	9	5		4	4	4
3.	Petrocrania hamiltoniae					1				
4.	Orbiculoidea media	15		6	3	4	8	9	15	
5.	Orthostrophia strophomen.									
6.	Rhipidomella		2	1	2	2				
7.	Tropidoleptus	14	23	15	50	7	2	5	4	1
8.	Protoleptostrophia									
9.	Megastrophia concava					1				
10.	Strophonella ampla	2								
11.	Schuchertella									
12.	Devonochonetes setigerus									
13.	Devonochonetes scitulus		1				1	1		
14.	Devonochonetes coronatus	1	3	3	2	7	1	2	1	3
15.	Longispina		1	2						
16.	Chonetes cf. lineatus	113	197	127	129	159	161	193	180	63
17.	Truncalosia truncata									
18.	Productella									
19.	Spinulicosta spinulicosta									1
20.	Camarotoecia congregata								1	
21.	"Leiorynchus" sp.	2	3	4	3	2		1	3	2
22.	Atrypa			2						
23.	Athyris spiriferoides					1				
24.	Ambocoelia umbonata	57	16	24	27	100	8	51	54	26
25.	Pustulatia									
26.	Cyrtina	2	6	3	2	15			5	4
27.	Delthyris sulcata			1						
28.	Mucrospirifer mucronatus	2	5	2		10	4	9	7	1
29.	Mucrospirifer consobrinus									
30.	Tylothyris mesocostalis	1	2	1	2	4	5	8	2	2
31.	Spinocyrtia granulosa									
32.	Mediospirifer									
33.	Elytha fimbriata									
34.	Rhipidothyris lepida									
35.	Tellinopsis									
36.	Nucula bellistriata									1
37.	Nucula corbuliformis	3	1	3	1	6	1		2	3
38.	Nucula lirata	2		1			1		1	1
39.	Nucula opima			2		1		1		
40.	Nuculites oblongatus	2	1		1	5			3	3
41.	Nuculites triqueter									
42.	Nuculites sp.									
43.	Palaeoneilo constricta									
44.	Palaeoneilo fecunda			1						

	Sampling Unit								
	73	74	75	76	77	78	79	80	81
45. Palaeoneilo halli									
46. Palaeoneilo marginata	4		1		3				
47. Palaeoneilo sp.									
48. Nuculana									
49. nuculoidea/nuculites									
50. Praecardium									
51. Buciola	1								
52. Pararca									
53. Lunulacardium curtum									
54. Pteriochaenia					2		1	1	
55. Mytilarca								1	
56. Leptodesma									
57. Leiopteria									
58. Ptychopteria boydi									
59. Actinopteria boydi					1				1
60. Nyassa									
61. Pterinopectin									
62. Pseudoaviculopectin									
63. Lyriopectin									
64. Aviculopectin									
65. pectinids									
66. Modiomorpha concentrica									
67. Modiomorpha mytiloides			1						
68. Modiomorpha subalata									
69. Goniophora pygmaea									
70. Modiella									
71. Cypricardella bellistriata?									
72. Cypricardinia									
73. Grammysia									
74. Grammysioidea									
75. Glossites					1				
76. Parallelodon				1					
77. Solemya					1				
78. bryozoans sp. 1									
79. bryozoans sp. 2									
80. Eliasopora stellata									
81. Reptaria									
82. cyclostomate									
83. Eridotrypella obliqua									1
84. trepostomate									
85. Loculipora									
86. Polypora incepta		2	2		6	1	3	2	
87. Unitrypa					1				
88. Sulcoretepora gilberti					2				52

	Sampling Unit								
	73	74	75	76	77	78	79	80	81
89. Taeniopora exigua									3
90. cryptostomate 1									
91. cryptostomate 2		1			8		1		
92. gastropods 1									
93. gastropods 2	1						1		
94. Cyrtolites									
95. "Bucania"									
96. Retispira leda									
97. Patellilabia lyra									
98. bellerophontid									
99. Straparollus laxus									
100. Mourlonia itys									
101. Mourlonia lucina									
102. Glyptomaria capillaria					2		1		1
103. Gyroma									
104. Holopea									
105. Naticonema									
106. Platyceras									
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.									
110. Dechenella									
111. Phacops rana	1				2	1		5	3
112. Greenops boothi	2	3	1	1	2			2	1
113. crinoids	p	p	p	p	p			p	p
114. Michelinoceras	p								
115. Striacoceras									
116. Spyroceras				p					
117. Bactrites									
118. Tornoceras									
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum									
123. Cladochonus dichotoma									
124. auloporids									
125. hyolithids								p	
126. Styliolina fissurella									
127. Tentaculites							p		
128. Coleolus									
129. Cornulites									
130. ostracodes									
131. Ponderodictya punctulifera									
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		82	83	84	85	86	87	88	89	90
1.	"Lingula"									
2.	Craniops hamiltoniae		1			1		4	1	
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media	1	5			5	5	7	2	
5.	Orthostrophia strophomen.									
6.	Rhipidomella vanuxemi	1				1			2	
7.	"Tropidoleptus"		1	1	1			1		
8.	Protoleptostrophia perplana									
9.	Megastrophia concava					3		1		
10.	Strophonella ampla									
11.	Schuchertella arctostriatus									
12.	Devonochonetes setigerus									
13.	Devonochonetes scitulus		3							
14.	Devonochonetes coronatus	1	1		1		2	1	2	
15.	Longispina mucronatus		1							
16.	Chonetes cf. lineatus	14	118	156	116	233	113	133	50	20
17.	Truncalosia truncata									
18.	Productella									
19.	Spinulicosta spinulicosta									
20.	Camarotoechia congregata									
21.	"Leiorynchus" sp.	3	3	4	4	4	5	6		
22.	Atrypa									
23.	Athyris spiriferoides							3		
24.	Ambocoelia umbonata	14	8	7	13	35	20	69	24	1
25.	Pustulatia									
26.	Cyrtina hamiltonensis	1		2	3	3	6	1	3	
27.	Megakoslowskiella sulcata									
28.	Mucrospirifer mucronatus			20	2	6		3	1	
29.	Mucrospirifer consobrinus							1		
30.	"Tylothyris"	1	1	5	4	9		5		
31.	Spinocyrtia granulosa									
32.	Mediospirifer									
33.	Elita fimbriata									
34.	"Rhipidothyris"									
35.	Tellinopsis subemarginata									
36.	Nucula bellistriata					1		2	1	
37.	Nucula corbuliformis		1	1	2	2			1	1
38.	Nucula lirata				1			1		
39.	Nucula opima		1		1	3		2		
40.	Nuculites oblongatus			4	2	1	1	3		
41.	Nuculites triqueter									
42.	Nuculites sp.									
43.	Palaeoneilo constricta									
44.	Palaeoneilo fecunda									

		Sampling Unit								
		82	83	84	85	86	87	88	89	90
45.	Palaeoneilo halli									
46.	Palaeoneilo marginata		1	1		1		1	2	
47.	Palaeoneilo sp.									
48.	Nuculana			1						
49.	nuculoidea/nuculites									
50.	Praecardium potens				1					
51.	Buchiola retrostriata									
52.	Pararca									
53.	Lunulacardium curtum			2						
54.	Pterchaenia fragilis			1						
55.	Mytilarca									
56.	Leptodesma conradi									
57.	Leiopteria									
58.	Ptychopteria boydi									
59.	Actinopteria boydi									
60.	Nyassa						1			
61.	Pterinopecten									
62.	Pseudoaviculopecten									
63.	Lyriopecten				1					
64.	Aviculopecten									
65.	pectinids									
66.	Modiomorpha concentrica									
67.	Modiomorpha mytiloides				1					
68.	Modiomorpha subalata									
69.	Goniophora pygmaea									
70.	Modiella pygmaea									
71.	Cypricardella bellistriata?									
72.	Cypricardinia indenta									
73.	Grammysia									
74.	Grammysioidea alveata									
75.	Glossites									
76.	Parallelodon hamiltoniae					1				
77.	Solemya vetusta									
78.	bryozoans sp. 1									
79.	bryozoans sp. 2							1		
80.	Eliasopora stellata									
81.	Reptaria									
82.	cyclostomate									
83.	Eridotrypella obliqua							1		
84.	trepostomate									
85.	Loculipora									
86.	Polypora incepta					2			3	
87.	Unitrypa scalaris									
88.	Sulcoretepora gilberti	5		1					40	1

	Sampling Unit 82	83	84	85	86	87	88	89	90
89. Taeniopora exigua									
90. cryptostomate 1									
91. cryptostomate 2						1		1	
92. gastropods 1									
93. gastropods 2			2				1	1	
94. "Cyrtolites"									
95. "Bucania"									
96. Retispira leda									
97. Patellilabia lyra									
98. bellerophontid									
99. Straparollus laxus						1			
100. Mourlonia itys									
101. Mourlonia lucina									
102. Glyptomaria capillaria							2	1	
103. Gyroma									
104. Holopea									
105. Naticonema									
106. Platyceras									
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.									
110. Dechenella									
111. Phacops rana			1		1	1	1	1	
112. Greenops boothi					6	5	3		
113. crinoids	p			p	p	p	p	p	p
114. Michelinoceras	p						p		
115. Striacoceras									
116. Spyroceras									
117. Bactrites									
118. Tornoceras									
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum									
123. Cladochonus dichotoma									
124. auloporids									
125. hyolithids									
126. Styliolina fissurella		p							
127. Tentaculites								p	
128. Coleolus									
129. Cornulites									
130. ostacodes									
131. Ponderodictya punctulifera									
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]								
		91	92	93	94	95	96	97	98	99
1.	"Lingula"									
2.	Craniops hamiltoniae			8	2	4		1	1	
3.	Petrocrania hamiltoniae									
4.	Orbiculoidea media	9	1	6		2				
5.	Orthostrophia strophomen.	1								
6.	Rhipidomella			2	1	1				
7.	Tropidoleptus	1		3	3					
8.	Protoleptostrophia									
9.	Megastrophia concava									
10.	Strophonella ampla		1			1				
11.	Schuchertella									
12.	Devonochonetes setigerus									
13.	Devonochonetes scitulus			1	1	2			4	6
14.	Devonochonetes coronatus	2		2	1	2	1	2		
15.	Longispina									
16.	Chonetes cf. lineatus	127	169	105	37	210	115	135		
17.	Truncalosia truncata									
18.	Productella									
19.	Spinulicosta spinulicosta					1	1			
20.	Camarotoecia congregata									
21.	"Leiorynchus" sp.	8	3	4	4	4	7	1		
22.	Atrypa									
23.	Athyris spiriferoides	1	1							
24.	Ambocoelia umbonata	20	24	31	16	10	9	5		
25.	Pustulatia									
26.	Cyrtina	4	3	8	4	4	4	1		
27.	Delthyris sulcata									
28.	Mucrospirifer mucronatus	2	1	1		9	9	10		
29.	Mucrospirifer consobrinus			1				1		
30.	Tylothyris mesocostalis	5	5	3	7	8	8	5		
31.	Spinocyrtia granulosa									
32.	Mediospirifer									
33.	Elytha fimbriata									
34.	Rhipidothyris lepida									
35.	Tellinopsis									
36.	Nucula bellistriata						2	1		
37.	Nucula corbuliformis	3	1	2	1	4	5	2		
38.	Nucula lirata		1	1		2				
39.	Nucula opima			1	2			1		
40.	Nuculites oblongatus	2	1	4		10	2	1		
41.	Nuculites triqueter	1								
42.	Nuculites sp.									
43.	Palaeoneilo constricta									
44.	Palaeoneilo fecunda									

		Sampling Unit								
		91	92	93	94	95	96	97	98	99
45.	Palaeoneilo halli									
46.	Palaeoneilo marginata					2	1			
47.	Palaeoneilo sp.									2
48.	Nuculana									
49.	nuculoidea/nuculites									
50.	Praecardium									
51.	Buciola									
52.	Pararca		1							
53.	Lunulacardium curtum		1	1	1		1			
54.	Pteriochaenia					1	2	1		
55.	Mytilarca									
56.	Leptodesma									
57.	Leiopteria					1				
58.	Ptychopteria boydi									
59.	Actinopteria boydi				1		1			
60.	Nyassa									
61.	Pterinopectin									
62.	Pseudoaviculopectin									
63.	Lyriopectin									
64.	Aviculopectin									
65.	pectinids									
66.	Modiomorpha concentrica			1						
67.	Modiomorpha mytiloides									
68.	Modiomorpha subalata									
69.	Goniophora pygmaea									
70.	Modiella									
71.	Cypricardella bellistriata?									
72.	Cypricardinia									
73.	Grammysia									
74.	Grammysioidea									
75.	Glossites									
76.	Parallelodon									
77.	Solemya									
78.	bryozoans sp. 1									
79.	bryozoans sp. 2	1								
80.	Eliasopora stellata									
81.	Reptaria									
82.	cyclostomate									
83.	Eridotrypella obliqua									
84.	trepostomate								2	
85.	Loculipora									
86.	Polypora incepta	2			1					
87.	Unitrypa									
88.	Sulcoretepora gilberti	6			13	1				

	Sampling Unit								
	91	92	93	94	95	96	97	98	99
89. Taeniopora exigua			1	2					
90. cryptostomate 1								1	
91. cryptostomate 2	2		1	2	1				
92. gastropods 1									
93. gastropods 2					1				
94. Cyrtolites									
95. "Bucania"									
96. Retispira leda									
97. Patellilabia lyra									
98. bellerophontid									
99. Straparollus laxus									
100. Mourlonia itys									
101. Mourlonia lucina						4			
102. Glyptomaria capillaria				3	2				
103. Gyroma									
104. Holopea									
105. Naticonema									
106. Platyceras									
107. Platystoma lineata									
108. "Elasmonema"									
109. Palaeozygopleura hamilton.	1								
110. Dechenella									1
111. Phacops rana			3						1
112. Greenops boothi		1	1				1		1
113. crinoids		p	p	p	p	p		p	p
114. Michelinoceras	p						p	p	p
115. Striacoceras					p				
116. Spyroceras			p						
117. Bactrites									
118. Tornoceras									
119. ammonoids									
120. sponges									
121. Conularia									
122. Stereolasma rectum									
123. Cladochonus dichotoma									
124. auloporids									
125. hyolithids					p		p		
126. Styliolina fissurella					p	p			
127. Tentaculites		p		p					
128. Coleolus			p	p	p	p			
129. Cornulites									
130. ostacodes									
131. Ponderodictya punctulifera									
132. Cyrtonella									

1. See Table 1.2 for localities.

TABLE 1.3

Sampling Unit Population Counts

		Sampling Unit[1]							
		100	101	102	103	104	105	106	107
1.	"Lingula"					1			
2.	Craniops hamiltoniae	1	3			1		2	
3.	Petrocrania hamiltoniae								
4.	Orbiculoidea media								
5.	Orthostrophia strophomen.								
6.	Rhipidomella								
7.	Tropidoleptus	28	62	33	12	23	17	79	132
8.	Protoleptostrophia								
9.	Megastrophia concava								
10.	Strophonella ampla								
11.	Schuchertella			1					
12.	Devonochonetes setigerus								
13.	Devonochonetes scitulus	3	4	3	4	2	4	4	1
14.	Devonochonetes coronatus								
15.	Longispina								
16.	Chonetes cf. lineatus								
17.	Truncalosia truncata								
18.	Productella								
19.	Spinulicosta spinulicosta								
20.	Camarotoecia congregata								
21.	"Leiorynchus" sp.								
22.	Atrypa								
23.	Athyris spiriferoides								
24.	Ambocoelia umbonata	46	79	112	40	60	19	99	81
25.	Pustulatia								
26.	Cyrtina	1					2		
27.	Delthyris sulcata								
28.	Mucrospirifer mucronatus								
29.	Mucrospirifer consobrinus								
30.	Tylothyris mesocostalis								
31.	Spinocyrtia granulosa								
32.	Mediospirifer								
33.	Elytha fimbriata								
34.	Rhipidothyris lepida								
35.	Tellinopsis								
36.	Nucula bellistriata								
37.	Nucula corbuliformis	1	2	16	28	20	1	11	18
38.	Nucula lirata								
39.	Nucula opima								
40.	Nuculites oblongatus				1				
41.	Nuculites triqueter				1	1			
42.	Nuculites sp.								
43.	Palaeoneilo constricta								
44.	Palaeoneilo fecunda								

		Sampling Unit							
		100	101	102	103	104	105	106	107
45.	Palaeoneilo halli								
46.	Palaeoneilo marginata								
47.	Palaeoneilo sp.	4	5				1		
48.	Nuculana								
49.	nuculoidea/nuculites								
50.	Praecardium								
51.	Buciola								
52.	Pararca								
53.	Lunulacardium curtum								
54.	Pteriochaenia	4	3	1			1	3	
55.	Mytilarca								
56.	Leptodesma								
57.	Leiopteria							1	
58.	Ptychopteria boydi								
59.	Actinopteria boydi								
60.	Nyassa								
61.	Pterinopectin								
62.	Pseudoaviculopectin								
63.	Lyriopectin								
64.	Aviculopectin	1	3	3	3	7	4	14	2
65.	pectinids			1			1		
66.	Modiomorpha concentrica								
67.	Modiomorpha mytiloides								
68.	Modiomorpha subalata								
69.	Goniophora pygmaea								
70.	Modiella								
71.	Cypricardella bellistriata?								
72.	Cypricardinia								
73.	Grammysia		1						
74.	Grammysioidea								
75.	Glossites								
76.	Parallelodon								
77.	Solemya								
78.	bryozoans sp. 1								
79.	bryozoans sp. 2								
80.	Eliasopora stellata								
81.	Reptaria						1		
82.	cyclostomate								
83.	Eridotrypella obliqua								
84.	trepostomate								
85.	Loculipora								
86.	Polypora incepta								
87.	Unitrypa								
88.	Sulcoretepora gilberti								

	Sampling Unit							
	100	101	102	103	104	105	106	107
89. Taeniopora exigua								
90. cryptostomate 1			2		4	10	59	30
91. cryptostomate 2								
92. gastropods 1								
93. gastropods 2								
94. Cyrtolites							1	
95. "Bucania"								
96. Retispira leda								
97. Patellilabia lyra								
98. bellerophontid			1	1	1			
99. Straparollus laxus								
100. Mourlonia itys		1		2	4	2	15	4
101. Mourlonia lucina								
102. Glyptomaria capillaria								
103. Gyroma								
104. Holopea								
105. Naticonema								
106. Platyceras								
107. Platystoma lineata								
108. "Elasmonema"								
109. Palaeozygopleura hamilton.		1		1		1		
110. Dechenella								
111. Phacops rana	1	1		1				
112. Greenops boothi	2	3	1	1	1	1	1	1
113. crinoids							p	
114. Michelinoceras	p	p	p	p	p	p	p	p
115. Striacoceras								
116. Spyroceras								
117. Bactrites				p	p	p	p	
118. Tornoceras			p	p	p	p	p	p
119. ammonoids								
120. sponges								
121. Conularia								
122. Stereolasma rectum								
123. Cladochonus dichotoma								
124. auloporids	p							
125. hyolithids								
126. Styliolina fissurella	p	p	p	p	p	p	p	p
127. Tentaculites								
128. Coleolus								
129. Cornulites		p						
130. ostacodes			p				p	p
131. Ponderodictya punctulifera								
132. Cyrtonella								

1. See Table 1.2 for localities.

TABLE 1.4

Taxon and Substrate-Mobility-Trophic Type

A "Phylum"
- b = Brachiopoda
- p = Mollusca (bivalves)
- e = Bryozoa
- g = Mollusca (gastropods)
- t = Arthropoda (trilobites)
- c = Echinodermata (crinoids)
- m = Mollusca (cephalopods)
- n = Porifera/Coelenterata
- w = "worms"
- o = ostracodes/monoplacophorans

B "Class"
- in = Inarticulata
- ar = Articulata
- bi = Bivalvia
- gy = Gymnolaemata
- ga = Gastropoda
- tr = Trilobita
- cr = Crinoidea
- ce = Cephalopoda
- sp = sponge
- sc = Scyphozoa
- an = Anthozoa
- wo = "worms"
- os = Ostracoda
- mo = Monoplacophora

C Genus

D Species

E Substrate
- i = infaunal
- e = epifaunal
- p = planktic

F Mobility
- i = unattached immobile
- m = unattached mobile
- l = attached low
- h = attached high
- v = attached mid to high
- s = swimmer

G Trophic
- s = suspension
- d = deposit
- g = grazer +/or scavenger
- e = coprophagus
- m = carnivore
- c = microcarnivore
- a = deposit +/or scavenger

		A	B	C	D	E	F	G
1.	"Lingula"	b	in	lin	lin	i	i	s
2.	Craniops hamiltoniae	b	in	cra	cra	e	i	s
3.	Petrocrania hamiltoniae	b	in	pet	pet	e	l	s
4.	Orbiculoidea media	b	in	orb	orb	e	l	s
5.	Orthostrophia strophomen.	b	ar	ort	ort	e	i	s
6.	Rhipidomella vanuxemi	b	ar	rhi	rhi	e	i	s
7.	"Tropidoleptus"	b	ar	tro	tro	e	i	s
8.	Protoleptostrophia perplana	b	ar	pro	pro	e	i	s
9.	Megastrophia concava	b	ar	meg	meg	e	i	s
10.	Strophonella ampla	b	ar	sto	sto	e	i	s
11.	Schuchertella arctostriatus	b	ar	sch	sch	e	i	s
12.	Devonochonetes setigerus	b	ar	dev	devt	e	i	s
13.	Devonochonetes scitulus	b	ar	dev	devs	e	i	s
14.	Devonochonetes coronatus	b	ar	dev	devc	e	i	s
15.	Longispina mucronatus	b	ar	lon	lon	e	i	s
16.	Chonetes cf. lineatus	b	ar	cho	cho	e	i	s
17.	Truncalosia truncata	b	ar	tru	tru	e	i	s
18.	Productella	b	ar	prd	prd	e	i	s
19.	Spinulicosta spinulicosta	b	ar	spi	spi	e	i	s
20.	Camarotoechia congregata	b	ar	cam	cam	e	l	s
21.	"Leiorynchus" sp.	b	ar	lei	lei	e	l	s
22.	Atrypa	b	ar	atr	atr	e	i	s
23.	Athyris spiriferoides	b	ar	ath	ath	e	l	s
24.	Ambocoelia umbonata	b	ar	amb	amb	e	l?	s
25.	Pustulatia	b	ar	pus	pus	e	l	s
26.	Cyrtina hamiltonensis	b	ar	cyr	cyr	e	l	s
27.	Megakoslowskiella sulcata	b	ar	del	del	e	i	s
28.	Mucrospirifer mucronatus	b	ar	muc	mucm	e	i	s
29.	Mucrospirifer consobrinus	b	ar	muc	mucc	e	i	s
30.	"Tylothyris"	b	ar	tyl	tyl	e	l	s
31.	Spinocyrtia granulosa	b	ar	spn	spn	e	i	s
32.	Mediospirifer	b	ar	med	med	e	l	s
33.	Elita fimbriata	b	ar	eli	eli	e	i	s
34.	"Rhipidothyris"	b	ar	rhp	rhp	e	l	s
35.	Tellinopsis subemarginata	p	bi	tel	tel	i	m	d
36.	Nucula bellistriata	p	bi	nuc	nucb	i	m	d
37.	Nucula corbuliformis	p	bi	nuc	nucc	i	m	d
38.	Nucula lirata	p	bi	nuc	nucl	i	m	d
39.	Nucula opima	p	bi	nuc	nuco	i	m	d
40.	Nuculites oblongatus	p	bi	nuu	nuuo	i	m	d
41.	Nuculites triqueter	p	bi	nuu	nuut	i	m	d
42.	Nuculites sp.	p	bi	nuu	nuuz	i	m	d
43.	Palaeoneilo constricta	p	bi	pal	palc	i	m	d
44.	Palaeoneilo fecunda	p	bi	pal	palf	i	m	d
45.	Palaeoneilo halli	p	bi	pal	palh	i	m	d
46.	Palaeoneilo marginata	p	bi	pal	palm	i	m	d
47.	Palaeoneilo sp.	p	bi	pal	palz	i	m	d
48.	Nuculana	p	bi	nua	nua	i	m	d
49.	nuculoidea/nuculites	p	bi	nul	nul	i	m	d
50.	Praecardium potens	p	bi	pra	pra	i	m	d

		A	B	C	D	E	F	G
51.	Buchiola retrostriata	p	bi	buc	buc	i	m	d
52.	Pararca	p	bi	pac	pac	i	m	d
53.	Lunulacardium curtum	p	bi	lun	lun	e	l	s
54.	Pterchaenia fragilis	p	bi	pte	pte	e	l	s
55.	Mytilarca	p	bi	myt	myt	e	l	s
56.	Leptodesma conradi	p	bi	lep	lep	e	l	s
57.	Leiopteria	p	bi	leo	leo	e	l	s
58.	Ptychopteria boydi	p	bi	pty	pty	e	l	s
59.	Actinopteria boydi	p	bi	act	act	e	l	s
60.	Nyassa	p	bi	nya	nya	e	l	s
61.	Pterinopecten	p	bi	ptr	ptr	e	l	s
62.	Pseudoaviculopecten	p	bi	pse	pse	e	l	s
63.	Lyriopecten	p	bi	lyr	lyr	e	l	s
64.	Aviculopecten	p	bi	avi	avi	e	l	s
65.	pectinids	p	bi	pec	pec	e	l	s
66.	Modiomorpha concentrica	p	bi	mod	modc	i	i	s
67.	Modiomorpha mytiloides	p	bi	mod	modm	i	i	s
68.	Modiomorpha subalata	p	bi	mod	mods	i	i	s
69.	Goniophora pygmaea	p	bi	gon	gon	i	i	s
70.	Modiella pygmaea	p	bi	moi	moi	i	m	s
71.	Cypricardella bellistriata?	p	bi	cyp	cyp	i	m	s
72.	Cypricardinia indenta	p	bi	cyi	cyi	i	m	s
73.	Grammysia	p	bi	gra	gra	i	m	s
74.	Grammysioidea alveata	p	bi	grm	grm	i	m	s
75.	Glossites	p	bi	glo	glo	i	m	s
76.	Parallelodon hamiltoniae	p	bi	par	par	e	l	s
77.	Solemya vetusta	p	bi	sol	sol	i	m	s
78.	bryozoans sp. 1	e	gy	bry	brym	e	l	s
79.	bryozoans sp. 2	e	gy	bry	bryp	e	l	s
80.	Eliasopora stellata	e	gy	els	els	e	l	s
81.	Reptaria	e	gy	rep	rep	e?	l	s
82.	cyclostomate	e	gy	cyc	cyc	e	l	s
83.	Eridotrypella obliqua	e	gy	eri	eri	e	l	s
84.	trepostomate	e	gy	tre	tre	e	l	s
85.	Loculipora	e	gy	loc	loc	e	l	s
86.	Polypora incepta	e	gy	pol	pol	e	l	s
87.	Unitrypa scalaris	e	gy	uni	uni	e	l	s
88.	Sulcoretepora gilberti	e	gy	sul	sul	e	l	s
89.	Taeniopora exigua	e	gy	tae	tae	e	l	s
90.	cryptostomate 1	e	gy	cry	cryb	e	l	s
91.	cryptostomate 2	e	gy	cry	cryp	e	l	s
92.	gastropods 1	g	ga	gas	gasm	e	m	g
93.	gastropods 2	g	ga	gas	gasp	e	m	g
94.	"Cyrtolites"	g	ga	cyo	cyo	e	m	g
95.	"Bucania"	g	ga	bua	bua	e	m	g
96.	Retispira leda	g	ga	ret	ret	e	m	g
97.	Patellilabia lyra	g	ga	pat	pat	e	m	g
98.	bellerophontid	g	ga	bel	bel	e	m	g
99.	Straparollus laxus	g	ga	str	str	e	m	g
100.	Mourlonia itys	g	ga	mou	moui	e	m	g

	A	B	C	D	E	F	G
101. Mourlonia lucina	g	ga	mou	moul	e	m	g
102. Glyptomaria capillaria	g	ga	gly	gly	e	m	g
103. Gyroma	g	ga	gyr	gyr	e	m	g
104. Holopea	g	ga	hol	hol	e	m	g
105. Naticonema	g	ga	nat	nat	e	h	e?
106. Platyceras	g	ga	pla	pla	e	h	e?
107. Platystoma lineata	g	ga	plt	plt	e	h	e?
108. "Elasmonema"	g	ga	ela	ela	e	m	g
109. Palaeozygopleura hamilton.	g	ga	paa	paa	e	m	g
110. Dechenella	t	tr	dec	dec	e	m	a
111. Phacops rana	t	tr	pha	pha	e	m	a
112. Greenops boothi	t	tr	gre	gre	e	m	a
113. crinoids	c	cr	cri	cri	e	v	s
114. Michelinoceras	m	ce	mic	mic	p	s	m
115. Striacoceras	m	ce	sti	sti	p	s	m
116. Spyroceras	m	ce	spy	spy	p	s	m
117. Bactrites	m	ce	bac	bac	p	s	m
118. Tornoceras	m	ce	tor	tor	p	s	m
119. ammonoids	m	ce	amm	amm	p	s	m
120. sponges	n	sp	spo	spo	e	i	s
121. Conularia	n	sc?	con	con	e	i	c?
122. Stereolasma rectum	n	an	ste	ste	e	i	c
123. Cladochonus dichotoma	n	an	cla	cla	e	i	c
124. auloporids	n	an	aul	aul	e	i	c
125. hyolithids	w	wo	hyo	hyo	e	m	a?
126. Styliolina fissurella	w	wo	sty	sty	p?	s?	c?
127. Tentaculites	w	wo	ten	ten	e	i	s?
128. Coleolus	w	wo	col	col	e	m	s?
129. Cornulites	w	wo	cor	cor	e	m	s?
130. ostacodes	o	os	ost	ost	e	m	c
131. Ponderodictya punctulifera	o	os	pon	pon	e	m	c
132. Cyrtonella	o	mo	cyt	cyt	e	m	d

TABLE 3.1

A Four Hierarchy Scheme[1]

all life on earth	biosphere (Suess, 1875)	abiotic earth	biogeographic system (Vernadsky, 1949 -- biosphere and Lovelock, 1979 -- Gaia)
	regional biota	regional abiota	regional-system
	community	local abiota	local-ecosystem
monophyletic taxon			
species			
deme	population		population-system
genome	phenome		organism-system
(sub-set of genome)	cell		cell-system
	organelle		organelle-system
gene	enzyme		metabolic pathway-system
		compounds molecules	
		gas/liquid/solid	
GENEALOGICAL	ECOLOGICAL	ABIOTIC	FUNCTIONAL
replicators units of selection ----------- evolution scalar	interactors levels of selection selective pressure development scalar	interactors ----------- selective pressure development scalar	self-organization: evolution/development and specification devel function circles scalar and specification

1. The entities noted are not entirely arbitrary as they are generally those that are of most interest to ecologists and evolutionary biologists.

TABLE 4.1

Sampling Units Grouped by Various Multivariate and Scaling Techniques[1,2]

	Cluster	PC-CORR	PC-COV	PC-COVN	Correlation
Equal Rock Volume (all)	4-6, 8-13, 24-26, 28, 31, 35, 38, 82, 90 7, 23, 34, 44 1-3 33, 36, 37, 41, 43, 45, 46	70-76, 78-81, 83-89, 91-97 59-64, 66-69, 106 48, 50, 54-56	71, 73-80, 83-88, 91-93, 95-97 15, 16, 18-21, 29 50, 54, 55, 65, 106, 107 31-33, 36, 37, 39-43, 45, 46, 48, 51 7, 17, 23, 30, 34, 44	71, 73-80, 83-88, 91-93, 95-97 15, 16, 18-20, 29 101, 102, 106, 107, 62, 64, 66, 50, 54, 55 32, 40, 41, 43, 45, 46, 48 6, 9-13, 22, 24-28 36-39, 42 7, 17, 23, 30, 34, 44	2, 4-6, 8-16, 18-22, 24-29 31, 33, 35-43, 45, 46, 51, 58 7, 17, 23, 30, 34, 44 52, 54-56 59-69 70-97 100-107, 49, 57
ERV (rares out)			71, 73-80, 83-88, 91-93, 95-97 15, 16, 18-21, 29 31, 33, 36, 37, 39, 42, 51, 58 32, 40, 41, 43, 45, 46, 48, 50 7, 17, 23, 34, 44		(same as ERV all)
Percentage (all)			70-97 7, 17, 23, 34, 44 4-6, 8-13, 15, 16, 18-22, 24-28 31-33, 35-41, 43, 45, 46, 51, 53, 58 59-69, 98-107, 57 52, 54-56, 47-50		(same as ERV all)
Presence/ Absence P/A (all)			70-89, 91-97 59-69 47, 48, 50, 52-56 100-107		59-69 100-107 (5, 6, 9-14, 18, 21, 22, 24-26) (33, 36, 41, 43, 45, 46) (70, 72-77, 79-81, 83, 86, 88, 93, 95, 97)

TABLE 4.1 continued

	PC-COV	Correlation
Octaves	70-97	4-6, 9-16, 18-22,
(all)	59-69	24-28
	100-107	31, 33, 36, 41, 43,
	49, 50, 52, 54-56	45, 46
		7, 17, 23, 34, 44
		52, 54-56
		59-69
		70-97
		100-107
Relative	70-97	4-6, 9-16, 18, 20-
Abundance	59-69	22, 24-28
Groups	100, 101, 103-106	31, 33, 36, 41, 43,
RAG (all)		45, 46
		7, 17, 23, 34, 44
		52, 54-56
		59, 61-69
		100-107
		70-89, 91-93, 95-
		97

1. See text for description of multivariate and scaling techniques.
2. See Tables 1.2 and 1.3 for sampling units, localities, and species counts.

TABLE 42

Correlation Values for Chonetes-Ambocoelia Community Type Based upon Equal Rock Volume

Sampling Unit	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	*
70	x	.94	.98	.96	.98	.99	.94	.94	.98	.99	.99	.78	.81	.98	.97	.99	.99	.99	.97	.79	.98	.99	.99	.99	.92	.98	.98	.98	.21(102)
71		x	.92	.99	.87	.92	.88	.99	.86	.95	.96	.77	.93	.87	.85	.89	.90	.91	.99	.79	.86	.91	.90	.95	.91	.86	.86	.85	.52(102)
72			x	.96	.98	.99	.99	.92	.96	.98	.97	.76	.78	.97	.95	.97	.97	.97	.94	.76	.96	.97	.97	.98	.91	.96	.96	.96	.28(101)
73				x	.92	.96	.93	.98	.91	.97	.98	.78	.90	.91	.89	.92	.94	.95	.99	.80	.90	.94	.93	.97	.92	.90	.90	.89	.44(102)
74					x	.99	.96	.88	.99	.98	.97	.75	.72	.99	.99	.99	.99	.99	.91	.75	.99	.99	.99	.97	.88	.99	.99	.99	.12(107)
75						x	.97	.92	.98	.99	.99	.71	.78	.99	.97	.99	.99	.99	.95	.77	.98	.99	.99	.99	.91	.98	.98	.98	.20(100)
76							x	.88	.92	.94	.93	.73	.74	.93	.91	.93	.93	.93	.90	.73	.92	.93	.93	.94	.87	.92	.92	.92	.38(107)
77								x	.86	.95	.96	.78	.93	.87	.86	.89	.91	.92	.99	.80	.86	.91	.91	.96	.92	.87	.87	.86	.50(102)
78									x	.98	.97	.74	.71	.99	.99	.99	.99	.99	.91	.74	.99	.99	.99	.97	.87	.99	.99	.99	.04(102)
79										x	.99	.78	.82	.98	.97	.99	.99	.99	.97	.79	.97	.99	.99	.99	.92	.97	.98	.97	.23(102)
80											x	.78	.84	.97	.96	.98	.99	.99	.98	.79	.96	.99	.98	.99	.92	.97	.97	.96	.26(102)
81												x	.84	.75	.74	.76	.76	.77	.78	.99	.77	.79	.76	.78	.92	.75	.74	.74	.28(102)
82													x	.72	.70	.75	.77	.79	.91	.87	.71	.79	.76	.84	.91	.71	.71	.70	.63(102)
83														x	.99	.99	.99	.99	.91	.75	.99	.99	.99	.97	.87	.99	.99	.99	.05(102)
84															x	.99	.99	.98	.90	.74	.99	.98	.99	.96	.86	.99	.99	.99	.06(40)
85																x	.99	.99	.93	.76	.99	.99	.99	.98	.89	.99	.99	.99	.09(102)
86																	x	.99	.94	.77	.99	.99	.99	.98	.90	.99	.99	.99	.13(102)
87																		x	.95	.77	.99	.99	.99	.99	.90	.99	.99	.98	.15(102)
88																			x	.80	.90	.94	.94	.98	.93	.91	.91	.90	.42(102)
89																				x	.77	.79	.77	.79	.92	.74	.74	.74	.32(102)
90																					x	.99	.99	.96	.88	.99	.99	.99	.05(103)
91																						x	.99	.98	.92	.99	.99	.99	.13(102)
92																							x	.98	.90	.99	.99	.99	.12(102)
93																								x	.93	.97	.97	.96	.26(102)
94																									x	.87	.88	.86	.35(102)
95																										x	.99	.99	.03(102)
96																											x	.99	.04(102)
97																												x	.17(102)

* next nearest value (sampling unit)

TABLE 4.3

Number of Correctly Identified Sampling Units Grouped into Proper Community Type by the Multivariate and Scaling Techniques Used in this Study[1]

Scaling	Multivariate Technique	"Leiorhy."-Devonocho. 24*	Devonocho.-Ambocoelia 17	Tropidolep.-Truncalosia 5	nuculid 6	Ambocoelia-Cran.-trepo. 11	Chonetes-Ambocoelia 28	Ambocoelia-Tropidoleptus 10
ERV	Cluster	13+5**	7	not id.	4	not id.	not id.	not id.
	PC-CORR	not id.	not id.	4+1	not id.	10+1	25	not id.
	PC-COVN	6/12***	6+1/5	not id.	6	not id.	21	4+6
	PC-COV	7	13+1	3+3	6	not id.	21	not id.
	Correlation	24	15	4	6	11	28	10
ERV (rares out)	PC-COV	7	6+2/8	not id.	5	not id.	21	not id.
	Correlation	24	15	4	6	11	28	10
Percentage	PC-COV	21	16	5+3	5	11+11	28	9+13
	Correlation	24	15	4	6	11	28	10
Presence/ Absence	PC-COV	not id.	not id.	5+3	not id.	11	27	8
	Correlation	14 (weak)	6 (weak)	not id.	not id.	11	16 (weak)	8
Octaves	PC-COV	not id.	not id.	5+1	not id.	11	28	8
	Correlation	21	7	4	5	11	28	8
Relative Abund. Grps.	PC-COV	not id.	not id.	not id.	not id.	11	28	6
	Correlation	20	7	4	5	10	26	8

* Number of sampling units in the identified community type.

** 13+5, etc. -- second value is number of sampling units not part of community type.

*** 6/12, etc. -- two separate groups identified from same community type.

1. See Table 4.1 and text for groupings and identification of community types.

TABLE 4.4

Performance of the Scaling and Multivariate Techniques Used in this Study in Identifying the Seven Community Types[1]

Scaling	Multivariate Technique	Not Identified	Poor*	Good**	Perfect
ERV	Cluster	4	3		
	PC-CORR	4		3	
	PC-COVN	2	3	1	1
	PC-COV	2	2	2	1
	Correlation			2	5
ERV (rares out)	PC-COV	3	2	2	
	Correlation			2	5
Percentage	PC-COV		3	3	1
	Correlation			2	5
Presence/ Absence	PC-COV	3	1	2	1
	Correlation	2	3	1	1
Octaves	PC-COV	3		2	2
	Correlation		1	4	2
Relative Abund. Grps.	PC-COV	4	1		2
	Correlation		1	6	

* poor: 2 groupings <u>or</u> >25% non-members <u>or</u> <70% members.
** *good*: ≥70% to <100% members

for PC-COV and Correlation:
Percentage > ERV > ERV (rares out) > Octaves > Rel. Abund. Grps. > Pres./Abs.

for ERV only:
Correlation > PC-COV > PC-COVN > PC-CORR > Cluster

for all:
Correlation > PC-COV

1. Based upon results given in Table 4.3.

TABLE 4.5

Simple Ranks (with percentages) of Three Most Abundant Species in each Sampling Unit[1]

S.U.	1	2	3	S.U.	1	2	3
1	lon 30.0	lei 17.3	lin/paa 10.0	41	devt 53.2	mucm 20.7	amb 19.7
2	lei 37.6	lon 18.1	orb 10.7	42	devt 62.4	mucm 10.2	amb 7.9
3	lon 30.0	devt 21.7	amb 18.3	43	devt 59.5	amb 16.3	mucm 14.4
4	lei 57.5	devt 24.5	amb 12.2	44	nul 92.0	devt 4.4	mods 2.8
5	lei 45.6	devt 25.0	amb 13.2	45	devt 64.4	amb 12.4	mucm 11.6
6	lei 78.7	devt 12.7	amb 5.5	46	devt 40.9	mucm 25.2	amb 23.7
7	nul 91.8	lei 6.2	mods 2.1	47	ath 16.3	sch 13.9	devt 12.0
8	lei 92.8	lin 3.6	paa 1.8	48	pha 54.0	gre 18.0	mucm 9.5
9	lei 65.9	devt 19.9	nul 10.9	49	amb 29.7	pse 17.3	tro 16.8
10	lei 50.2	devt 36.4	amb 6.9	50	tro 18.5	rhp 18.5	devt 15.8
11	lei 49.6	devt 32.7	amb 8.6	51	devt 60.3	mucm 20.5	pha 9.2
12	lei 61.7	devt 35.6	pte 1.1	52	tru 33.6	tro 20.5	devt 17.0
13	lei 45.3	devt 28.1	amb 15.8	53	devt 21.8	orb 16.2	mucm 14.1
14	lei 36.8	devt 32.7	amb 24.9	54	tro 37.4	tru 31.1	devt 9.5
15	lei 48.6	devt 32.0	amb 14.9	55	tru 35.5	tro 31.8	devt 9.0
16	lei 48.3	devt 39.9	cam 2.9	56	tro 25.3	tru 25.3	devt 14.5
17	nul 94.1	devt 3.8	lon 1.3	57	amb 52.6	tro 23.7	gly 7.4
18	lei 49.9	devt 35.7	cam 6.8	58	devt 54.9	mucm 38.9	pro 4.9
19	lei 49.0	devt 45.8	nat 4.9	59	devc 27.3	cra 23.5	amb 17.4
20	lei 56.8	devt 38.6	amb 4.4	60	cra 61.6	amb 17.6	gre 3.2
21	lei 55.8	devt 25.5	cam 6.2	61	amb 32.0	cra 12.0	devc/nucc 6.7
22	lei 39.9	devt 32.0	gasm 11.0	62	amb 47.8	paa 15.7	tre 9.6
23	nul 88.5	lei 11.5	------	63	cra 38.5	amb 26.4	tre 13.7
24	lei 46.6	devt 31.1	amb 9.8	64	amb 33.8	cra 27.9	tre 14.8
25	lei 47.9	devt 36.4	amb 6.6	65	amb 38.3	cra 24.4	tre 12.1
26	devt 43.2	lei 36.0	cam 6.1	66	pus 26.0	amb 24.9	tre 15.1
27	devt 45.5	lei 40.1	cam 8.0	67	tre 28.8	pus 26.1	amb 9.0
28	lei 65.3	devt 29.1	cam 4.0	68	tre 16.4	amb 15.5	paa 11.5
29	lei 28.9	devt 25.6	amb 12.8	69	devc 57.7	amb 15.0	mucm 7.3
30	nul 47.2	nuuo 13.0	str 11.4	70	cho 68.4	amb 16.0	cyr 3.2
31	devt 63.5	amb 19.8	mucm 8.3	71	cho 45.0	amb 29.2	orb 3.9
32	devt 40.9	rhp 30.7	tru 11.9	72	cho 59.5	tro 13.4	amb 13.0
33	devt 51.6	mucm 18.3	amb 8.7	73	cho 49.3	amb 24.9	orb 6.6
34	nul 97.4	str 2.6	-------	74	cho 73.5	tro 8.6	amb 6.0
35	devt 52.6	amb 23.4	lei 15.3	75	cho 61.7	amb 11.7	tro 7.3
36	devt 55.6	amb 20.5	mucm 17.1	76	cho 55.4	tro 21.5	amb 11.6
37	devt 52.0	amb 19.8	mucm 10.8	77	cho 44.4	amb 27.7	cyr 4.2
38	devt 46.6	amb 27.9	lei 21.0	78	cho 83.0	orb 4.1	amb 4.1
39	devt 41.7	amb 28.8	lei 8.5	79	cho 66.3	amb 17.5	orb/mucm 3.1
40	devt 36.1	mucm 22.2	amb 17.6	80	cho 61.4	amb 18.4	orb 5.1

TABLE 4.5 continued

S.U.	1	2	3
81	cho 36.0	sul 29.7	amb 14.3
82	cho 34.1	amb 34.1	sul 12.2
83	cho 81.4	amb 5.5	orb 3.4
84	cho 74.6	mucm 9.6	amb 3.3
85	cho 75.8	amb 8.4	lei/tyl 2.6
86	cho 73.3	amb 11.0	tyl 2.8
87	cho 70.2	amb 12.4	cyr 3.7
88	cho 52.6	amb 27.3	orb 2.8
89	cho 36.8	sul 29.4	amb 17.6
90	cho 87.0	amb 4.3	nucc/sul 4.3
91	cho 64.1	amb 10.1	orb 4.5
92	cho 79.0	amb 11.2	tyl 2.3
93	cho 55.0	amb 16.2	cra/cyr 4.2
94	cho 36.3	amb 15.7	sul 12.7
95	cho 74.2	amb 3.5	nuuo 3.5
96	cho 72.2	amb 4.4	mucm 4.4
97	cho 80.4	mucm 6.0	amb/tyl 3.0
98	devs 50.0	tre 25.0	cra/cryb 12.5
99	devs 54.5	palz 18.2	dec/pha/gre 9.1
100	amb 50.0	tro 30.4	palz/pte 4.3
101	amb 47.0	tro 36.9	palz 3.0
102	amb 64.4	tro 19.0	nucc 9.2
103	amb 42.1	nucc 29.5	tro 12.6
104	amb 48.0	tro 18.4	nucc 16.0
105	amb 29.2	tro 26.2	cryb 15.4
106	amb 34.3	tro 27.3	cryb 20.4
107	tro 49.1	amb 30.1	cryb 11.2

1. See Table 1.4 for code for each species.

TABLE 4.6

Simple Ranks of Three Most Abundant Species for each Sampling Unit Organized by Community Type[1]

Community Type	Species	Dominant	#2	#3	
"Leiorhynchus"-Devonochonetes 24*	*"Leiorhynchus"*	22**	2		8 additional species occur 1 time each among top three per sampling unit
	Devonocho. setigerus	2	20		
	Ambocoelia			12	
	Camarotoechia			6	
Devonochonetes-Ambocoelia 17	*Devonocho. setigerus*	17			5 species occur 1 time
	Ambocoelia		8	5	
	Mucrospirifer mucronatus		7	6	
	"Leiorhynchus"			3	
Tropidoleptus-Truncalosia 5	*Tropidoleptus*	3	2		1 species occurs 1 time
	Truncalosia	2	2		
	Devonocho. setigerus			5	
nuculid 6	nuculids	6			4 species occur 2 times; 2 occur 1 time
Ambocoelia-Craniops-trepostomate 11	*Ambocoelia*	4	5	2	1 species occurs 3 times; 2 occur 2 times; 3 occur 1 time
	Craniops	2	4		
	trepostomate	2		5	
Chonetes-Ambocoelia 28	*Chonetes*	28			1 species occurs 5 times; 4 occur 4 times; 3 occur 1 time
	Ambocoelia		20	8	
	Orbiculoidea		1	7	
Ambocoelia-Tropidoleptus 10	*Ambocoelia*	9	1		2 species occur 3 times; 1 occurs 2 times; 3 occur 1 time
	Tropidoleptus	1	7	2	

* Number of sampling units in community type.

** Number of sampling units species appears in for particular dominance category.

1. Based upon results given in Table 4.5

TABLE 4.7

Species Grouped by Community Type for Frequency of Occurrence in Sampling Units and Relative Abundance
(first number = % of total organism count of community type / second number = % of sampling units found in)

		Chonetes-Ambo.	"Leio."-Devono.	Devono.-Ambo.	Tropido-Trunca.	nuculid	Ambo-Cran.-trep.	Ambo-Tropido.
1.	"Lingula"		0.1-21				1.6-91	0.1-10
2.	Craniops hamiltoniae	1.3-68	0.1-13				19.0-100	0.5-40
3.	Petrocrania hamiltoniae	<0.1-4						
4.	Orbiculoidea media	2.0-71	0.1-4	0.6-18	<0.1-20		<0.1-9	
5.	Orthostrophia strophomen.	0.1-7						
6.	Rhipidomella vanuxemi	0.3-39		0.2-6	0.1-20			
7.	"Tropidoleptus"	3.4-68		0.3-12	27.6-100			29.4-100
8.	Protoleptostrophia perplana			0.2-12			<0.1-9	
9.	Megastrophia concava	0.1-11						
10.	Strophonella ampla	0.2-18						
11.	Schuchertella arctostriatus		0.3-21	1.0-29	0.2-60		1.4-55	0.1-10
12.	Devonochonetes setigerus		32.1-100	48.5-100	12.9-100	1.8-50		0.4-10
13.	Devonochonetes scitulus	0.2-29						1.8-80
14.	Devonochonetes coronatus	0.9-86					10.0-100	
15.	Longispina mucronatus	0.1-14	1.0-17	<0.1-6		0.2-17	1.8-73	
16.	Chonetes cf. lineatus	62.2-100						
17.	Truncalosia truncata		0.4-8	1.2-6	21.4-100			
18.	Productella						<0.1-9	
19.	Spinulicosta spinulicosta	<0.1-11						
20.	Camarotoechia congregata	<0.1-4	2.7-38		<0.1-20			
21.	"Leiorhynchus" sp.	1.4-89	48.8-100	4.9-35		3.9-33		
22.	Atrypa	<0.1-7					<0.1-9	
23.	Athyris spiriferoides	0.2-21		0.3-6				
24.	Ambocoelia umbonata	14.5-100	7.5-79	15.9-82	5.9-60	0.4-33	26.5-100	41.9-100
25.	Pustulatia				0.2-20		6.5-55	
26.	Cyrtina hamiltonensis	1.9-86					<0.1-18	0.2-20
27.	Megakoslowskiella sulcata	<0.1-4						
28.	Mucrospirifer mucronatus	1.7-79	2.4-38	14.6-88	8.2-100		1.8-82	0.9-20
29.	Mucrospirifer consobrinus	<0.1-11						
30.	"Tylothyris"	1.7-89						

Table 4.7 continued

		Chonetes-Ambo.	"Leio."-Devono.	Devono.-Ambo.	Tropido-Trunca.	nuculid	Ambo-Cran.-trep.	Ambo-Tropido
31.	Spinocyrtia granulosa		0.1-17	0.2-6			<0.1-18	
32.	Mediospirifer						<0.1-9	
33.	Elita fimbriata	<0.1-4						
34.	"Rhipidothyris"			3.1-6	5.6-20			
35.	Tellinopsis subemarginata				0.1-20	0.4-17	<0.1-9	
36.	Nucula bellistriata	0.2-29						
37.	Nucula corbuliformis	0.9-86					1.7-91	6.9-80
38.	Nucula lirata	0.2-39						
39.	Nucula opima	0.3-46						
40.	Nuculites oblongatus	0.9-71	<0.1-4	<0.1-6	0.3-40	1.2-17	0.2-55	0.1-10
41.	Nuculites triqueter	<0.1-7					<0.1-9	0.1-20
42.	Nuculites sp.			0.1-12				
43.	Palaeoneilo constricta					0.7-17	0.9-82	
44.	Palaeoneilo fecunda	<0.1-4					1.3-82	
45.	Palaeoneilo halli		<0.1-8		0.5-60			
46.	Palaeoneilo marginata	0.4-43		<0.1-6	<0.1-20		0.2-27	
47.	Palaeoneilo sp.						0.4-45	0.7-30
48.	Nuculana	<0.1-4						
49.	nuculoidea/nuculites		0.5-33	0.3-24	0.5-60	88.1-100		
50.	Praecardium potens	<0.1-4		<0.1-6		0.3-17		
51.	Buchiola retrostriata	<0.1-4			<0.1-20			
52.	Pararca	<0.1-4						
53.	Lunulacardium curtum	0.1-18	<0.1-4					<0.1-10
54.	Pterchaenia fragilis	0.2-29	0.8-75	3.0-76	1.1-80	0.1-17	1.3-91	0.9-60
55.	Mytilarca	<0.1-4	<0.1-8					
56.	Leptodesma conradi			0.1-6	0.1-40			
57.	Leiopteria	<0.1-4						0.1-10
58.	Ptychopteria boydi		<0.1-4	<0.1-12	0.6-80			0.1-10
59.	Actinopteria boydi	0.1-18						
60.	Nyassa	<0.1-4						
61.	Pterinopecten				0.5-40			0.2-20
62.	Pseudoaviculopecten			<0.1-6	1.7-40			0.8-10
63.	Lyriopecten	<0.1-4						
64.	Aviculopecten						<0.1-9	2.6-80
65.	pectinids						<0.1-18	0.1-20

Table 4.7 continued

		Chonetes-Ambo.	"Leio."-Devono.	Devono.-Ambo.	Tropido-Trunca.	nuculid	Ambo-Cran.-trep.	Ambo-Tropido.
66.	Modiomorpha concentrica	<0.1-4						
67.	Modiomorpha mytiloides	0.1-11						
68.	Modiomorpha subalata		0.2-17	0.4-29	0.4-80	0.8-33		
69.	Goniophora pygmaea					0.1-17		
70.	Modiella pygmaea				0.2-40		0.3-64	
71.	Cypricardella bellistriata?		<0.1-4	<0.1-6	<0.1-20			
72.	Cypricardinia indenta						0.3-36	
73.	Grammysia						0.2-36	0.1-10
74.	Grammysioidea alveata				<0.1-20	0.2-17		
75.	Glossites	<0.1-4						
76.	Parallelodon hamiltoniae	<0.1-7						
77.	Solemya vetusta	<0.1-4						
78.	bryozoans sp. 1		<0.1-4					
79.	bryozoans sp. 2	<0.1-7						
80.	Eliasopora stellata			<0.1-6				
81.	Reptaria				1.5-20			0.1-10
82.	cyclostomate		<0.1-4	0.4-18	1.8-80			
83.	Eridotrypella obliqua	<0.1-7						
84.	trepostomate						12.0-73	
85.	Loculipora						<0.1-9	
86.	Polypora incepta	0.4-39						
87.	Unitrypa scalaris	<0.1-4						
88.	Sulcoretepora gilberti	1.9-32						
89.	Taeniopora exigua	0.1-7						
90.	cryptostomate 1							7.5-50
91.	cryptostomate 2	0.3-36						
92.	gastropods 1		0.5-4					
93.	gastropods 2	0.1-21						
94.	"Cyrtolites"						<0.1-18	0.1-10
95.	"Bucania"			<0.1-6				
96.	Retispira leda		0.3-42	2.2-71	0.9-90	0.1-17		
97.	Patellilabia lyra				<0.1-20			
98.	bellerophontid						0.2-55	0.2-30
99.	Straparollus laxus	<0.1-4	<0.1-4	0.1-18		1.4-33		
100.	Mourlonia itys						2.3-100	2.0-60

Table 4.7 continued

		Chonetes-Ambo.	"Leio."-Devono.	Devono.-Ambo.	Tropido-Trunca.	nuculid	Ambo-Cran.-trep.	Ambo-Tropido.
101.	Mourlonia lucina	0.1-4						
102.	Glyptomaria capillaria	0.3-32	<0.1-4	0.2-6	0.8-60			0.3-10
103.	Gyroma							0.2-10
104.	Holopea		<0.1-4					
105.	Naticonema	<0.1-4	0.3-4					
106.	Platyceras		0.1-13	<0.1-6	<0.1-20		0.1-18	
107.	Platystoma lineata			<0.1-6	0.4-60			
108.	"Elasmonema"				<0.1-20			<0.1-10
109.	Palaeozygopleura hamilton.	<0.1-4	0.4-33	0.2-12	0.9-80		4.7-100	0.2-30
110.	Dechenella							
111.	Phacops rana	0.4-50	0.5-50	1.1-65	4.0-100		2.0-100	0.6-40
112.	Greenops boothi	0.5-54	0.7-63	0.7-47	1.6-80		2.6-100	0.8-80
113.*	crinoids	-79	-25	-53	-100		-36	-20
114.	Michelinoceras	-21	-46	-47	-80	-17	-91	-80
115.	Striacoceras	-4						
116.	Spyroceras	-11	-4				-9	
117.	Bactrites						-9	-40
118.	Tornoceras		-21	-18			-100	-60
119.	ammonoids	-4						
120.	sponges						-18	
121.	Conularia						-18	
122.	Stereolasma rectum		-4					
123.	Cladochonus dichotoma		-42	-12	-80			
124.	auloporids						-18	-10
125.	hyolithids	-11					-9	
126.	Styliolina fissurella	-14	-100	-88	-80	-17	-73	-90
127.	Tentaculites	-14	-96	-65	-20	-17		
128.	Coleolus	-14						
129.	Cornulites						-9	-10
130.	ostracodes		-8	-82	-60	-17	-27	-30
131.	Ponderodictya punctulifera		-100	-88	-100	-17		
132.	Cyrtonella							-10

* Species 113 to 132: % of sampling units found in.

TABLE 4.8

Species Grouped by Community Type that Show either a Relatively High or a Relatively Low Sampling Unit Appearance to Relative Abundance Ratio[1]

Community Type	Ratios*	Species
"Leiorhynchus"-Devonochonetes 33**	≥ 125	*Retispira* (140)
	≤ 30	*Longispina* (17), *Truncalosia* (20), *Camaroetoechia* (14), *Mucrospirifer m.* (16), gastropods 1 (8), *Naticonema* (13)
Devonochonetes-Ambocoelia 36	≥ 125	
	≤ 30	*Orbiculoidea* (30), *Rhipidomella* (30), *Schuchertella* (29), *Truncalosia* (5), *Athyris* (20), *Spinocyrtia* (30), *Rhipidothyris* (2), *Glyptomaria* (30)
Tropidoleptus-Truncalosia 37	≥ 125	*Schuchertella* (300), *Nuculites o.* (133), *Leptodesma* (400), *Ptychopteria* (133), *Modiomorpha s.* (200), *Modiella* (200), *Platystoma* (150)
	≤ 30	*Rhipidothyris* (4), *Pseudoaviculopectin* (24), *Reptaria* (13)
nuculid 15	≥ 125	
	≤ 30	*"Leiorhynchus"* (8), *Nuculites o.* (14), *Palaeoneilo c.* (24), *Straparollus* (24)
Ambocoelia-Craniops-trepostomate 38	≥ 125	*Nuculites o.* (275), *Palaeoneilo m.* (135), *Modiella* (213), *Grammysia* (180), bellerophontid (275)
	≤ 30	
Chonetes-Ambocoelia 63	≥ 125	*Rhipidomella* (130), *Devonochonetes sc.* (145), *Nucula b.* (145), *Nucula l.* (195), *Nucula o.* (153), *Pteriochaenia* (145), *Phacops* (125)
	≤ 30	*Sulcoretepora* (17)
Ambocoelia-Tropidoleptus 33	≥ 125	bellerophontid (150)
	≤ 30	*Devonochonetes se.* (25), *Mucrospirifer m.* (22), *Pseudoaviculopectin* (13)

* Ratios of sampling unit appearance % to abundance %:
≥ 125 = many sampling units / few in number (must be present in greater than 25 % of sampling units)
≤ 30 = few sampling units / many in number (must be present in less than 25 % of sampling units)

** Number of species identified in particular community type.

1. Based upon results given in Table 4.7.

TABLE 4.9

Number of Species Grouped by Community Type that Are either Characteristic or Ubiquitous[1]

Community Type	Total Species*	Characteristic	Characteristic / Sampling Unit	Total Species / Sampling Unit
"Leiorhynchus"-Devonochonetes	43	4 (9%)	4 / 24 (17%)	43 / 24 (179%)
Devonochonetes-Ambocoelia	44	3 (7%)	3 / 17 (18%)	44 / 17 (259%)
Tropidoleptus-Truncalosia	44	1 (2%)	1 /5 (20%)	44 / 5 (880%)
nuculid	20	1 (5%)	1 / 6 (17%)	20 / 6 (333%)
Ambocoelia-Cran.-trepost.	50	7 (14%)	7 / 11 (64%)	50 / 11 (455%)
Chonetes-Ambocoelia	72	35 (49%)	35 /28 (125%)	72 /28 (257%)
Ambocoelia-Tropidoleptus	42	3 (7%)	3 / 10 (30%)	42 / 10 (420%)

* Includes species identified but not precisely counted.

Characteristic: found in only one community type (see Table 4.7 for species names).
Ubiquitous: found in all community types or in all except nuculid community type (see text)
Ambocoelia, Mucrospirifer m., Nuculites o., Pteriochaenia, Phacops, Greenops,Palaeozygopleura, crinoids, *Michelinoceras, Styliolina*

1. Based upon results given in Table 4.7.

TABLE 4.10

"Niche" Distribution in Community Types (%)

	nuculid	Ambo-Tropido.	Ambo-Cran.-trep.	Tropido-Truncal.	Devono-Ambo.	"Leiorhyn"-Devono.	Chonetes-Ambo.
Epifaunal-Mobile-Grazer	1.5	3.0	7.2	2.6	2.7	1.2	0.5
Epifaunal-Mobile-Deposit Feeder	X	1.4	4.6	5.6	1.8	1.2	0.9
Infaunal-Mobile-Deposit Feeder	90.7	7.8	4.7	1.4	0.5	0.5	3.0
Epifaunal-Immobile-Suspension Feeder	2.0	32.6	34.0	70.5	66.2	39.0	69.2
Epifaunal-Low-Suspension Feeder	4.4	54.3	46.3	19.1	28.4	57.9	25.1
Infaunal-Immobile-Suspension Feeder	0.9	0.6	1.6	0.4	0.4	0.4	1.4
Infaunal-Mobile-Suspension Feeder	0.2	0.1	0.8	0.2	<0.1	<0.1	0.1

TABLE 4.11

Community Types for McCollum Sampling Units

(30)	nuculid	58	Devonochonetes-Ambocoelia
29*	"Leiorhynchus"-Devonochonetes	(57)	Ambocoelia-Tropidoleptus
28*	L-D	56	Tropidoleptus-Truncalosia
27*	L-D	55	T-T
26*	L-D	54	T-T
25*	L-D	53*	Devonochonetes-Ambocoelia
24*	L-D	52	Tropidoleptus-Truncalosia
(23)	nuculid	(+)	nuculid
22*	"Leiorhynchus"-Devonochonetes	51*	Devonochonetes-Ambocoelia
(+)	not counted	50	Tropidoleptus-Truncalosia
21*	"Leiorhynchus"-Devonochonetes	(49)	Ambocoelia-Tropidoleptus
20	L-D	48	trilobite
19	L-D	(47)	Athyris-Schuchertella
(+)	uncounted	46	Devonochonetes-Ambocoelia
18	"Leiorhynchus"-Devonochonetes	45	D-A
(17)	nuculid	(44)	nuculid
16	"Leiorhynchus"-Devonochonetes	43	Devonochonetes-Ambocoelia
15	L-D	42	D-A
14	L-D	(+)	uncounted
13	L-D	41	Devonochonetes-Ambocoelia
12	L-D	40	D-A
11*	L-D	(+)	uncounted
10*	L-D	39	Devonochonetes-Ambocoelia
(+)	uncounted	38	D-A
9*	"Leiorhynchus"-Devonochonetes	37	D-A
8*	L-D	36	D-A
(7)	nuculid	35	D-A
6*	"leiorhynchus"-Devonochonetes	(34)	nuculid
5*	L-D	33	Devonochonetes-Ambocoelia
4*	L-D	32	D-A
3	Longispina-Lingula	31	D-A
2*	"Leiorhynchus"-Devonochonetes		
1	Longispina-Lingula		

( ) = thin layer sample
* = assemblage characterized differently by McCollum (1980)

TABLE 5.1

Correlation Values of Sampling Units Using Pearson Product Moment For Community Types Investigated For Niche Related Structure[1]

"Leiorhynchus"-Devonochonetes *

Sampling Units[2]	r-value
E4 24-29	>0.86
E3 18-22	>0.93
E2 9-16	>0.80
E1 4-6	>0.92

* 22 sampling units always correlated among each other at >0.74 for each.

Chonetes-Ambocoelia **

Sampling Units[2]	r-value
E6 70, 72, 74, 76, 78, 85, 92	>0.92
E5 71, 73, 75, 77, 79, 86	>0.90
E4 80, 88, 93	>0.97
E3 81, 89, 94	>0.92
E2 82, 90, 95	>0.70
E1 84, 91, 97	>0.98

** 25 sampling units always correlated among each other at >0.70 for each.

1. See Chapter 4 for further criteria for distinguishing these as community types.
2. E1 (Environment 1) represents oldest fossils, then E2, etc. Each environment is made up of a series of closely associated sampling units (habitats) -- e.g., from the same bedding plane or bryozoan layer in nearby quarries or sequentially in a sampling regime. Besides this temporal and/or geographic association, various criteria (including the reported r-values) show them to be quite similar in fossil population patterns. See Table 1.2 for sampling unit locations and Appendix 5.2 for fossil counts.

TABLE 5.2

"*Leiorhynchus*"-*Devonochonetes* Coefficient of Variation Monte Carlo Analysis

		Random Generated Data (99 sets of 4)			Field Data
	Field CV	Mean CV	SD	Range	Rank (1 - 100)
7-1[1]	17.87%	19.71%	9.93%	4.50-49.94%	47
7-2	81.04	20.98	11.66	3.74-64.46	100*
7-3	9.89	21.92	9.97	5.81-50.02	12
7-4	53.51	21.39	9.24	4.08-49.63	100*
7-5	43.29	20.05	9.63	3.32-52.79	98*
13-1	35.04	26.54	14.23	6.45-110.17	79
13-2	73.70	28.18	13.50	2.33-61.47	100*
13-3	27.89	28.55	13.50	3.13-69.26	48
13-4	57.32	28.33	11.90	8.72-64.05	99*
13-5	78.26	28.40	11.56	6.81-57.65	100*
15-1	9.22	14.38	9.72	2.58-47.60	36
15-2	67.22	12.18	8.37	1.27-47.66	100*
15-3	6.33	12.83	8.06	1.00-47.34	22
15-4	21.55	13.12	7.79	1.60-40.06	87
15-5	57.01	12.89	8.46	2.55-44.60	100*
8[2]	13.39	12.96	3.34	5.42-21.19	59
11	31.08	11.52	4.46	1.78-21.60	100*
14	2.30	9.01	3.73	1.23-27.44	5*
16	25.52	3.28	2.31	0.32-13.89	100*
18	20.90	2.65	1.97	0.46-12.22	100*

1. Niche equation 7, etc. for population 1, etc. See Appendices 5.1 and 5.2 for niche equations, sampling units, and populations.
2. Niche equation 8, etc. for community.

Populations:
1. *Devonochonetes setigerus*
2. *Camarotoechia congregata*
3. *"Leiorhynchus" sp.*
4. *Ambocoelia umbonata*
5. *Mucrospirifer mucronatus*

TABLE 5.3

***Chonetes-Ambocoelia* Coefficient of Variation Monte Carlo Analysis**

	Field CV	Random Generated Data (99 sets of 6) Mean CV	SD	Range	Field Data Rank (1 - 100)
7-1[1]	46.59%	19.33%	10.37%	5.60-50.28%	97*
7-2	54.06	20.20	10.35	2.59-51.28	100*
7-3	5.00	21.02	10.23	4.20-54.59	2*
7-4	26.56	18.57	10.25	4.58-47.74	83
7-5	24.53	20.05	9.63	3.32-52.79	64
7-6	7.30	19.97	10.86	3.77-54.50	5*
7-7	21.39	20.46	8.61	2.94-47.62	62
7-8	111.24	19.11	10.07	3.60-51.56	100*
13-1	54.39	29.45	11.29	9.49-59.31	98*
13-2	130.38	28.84	10.55	7.60-61.82	100*
13-3	21.90	28.01	11.55	3.73-69.06	32
13-4	47.77	27.67	11.83	5.17-65.03	94
13-5	19.36	28.88	11.75	4.00-62.96	24
13-6	90.33	28.33	12.46	6.63-71.61	100*
13-7	51.54	27.42	10.06	7.57-50.03	100*
13-8	179.43	28.26	10.63	8.46-62.50	100*
15-1	5.88	9.77	7.87	1.40-39.47	30
15-2	50.99	9.87	7.25	1.90-39.69	100*
15-3	2.68	9.80	7.23	2.42-38.78	3*
15-4	19.61	8.64	5.52	2.17-32.15	94
15-5	9.30	8.97	5.52	2.95-34.43	67
15-6	12.10	9.10	6.36	1.57-39.35	85
15-7	11.27	9.02	5.45	2.14-40.39	75
15-8	92.14	9.55	6.85	1.92-39.42	100*
8[2]	11.07	13.19	2.59	8.84-19.35	26
11	12.01	9.36	2.52	2.37-13.82	85
14	2.95	8.28	1.74	2.99-11.94	1*
16	10.48	2.59	1.56	0.25-8.37	100*
18	20.39	2.02	0.87	0.43-4.58	100*

1. Niche equation 7, etc. for population 1, etc. See Appendices 5.1 and 5.2 for niche equations, sampling units, and populations.
2. Niche equation 8, etc. for community.

Populations:
1. *Orbiculoidea medea*
2. *Tropidoleptus*
3. *Chonetes cf. lineatus*
4. *Ambocoelia umbonata*
5. *Cyrtina*
6. *Mucrospirifer mucronatus*
7. *"Tylothyris"*
8. *Sulcoretepora gilberti*

TABLE 5.4

Field Data Values Compared to Sets of 99 Random Generated Data (summary results)

Total Field Data Values Ranked 1-5 or 96-100[1]

	Community Measures[2]	Population Measures[2]	Total
"Leiorhynchus"-Devonochonetes	17/20 (85%)	35/60 (56%)	52/80 (65%)
Chonetes-Ambocoelia	25/30 (83%)	69/144 (48%)	94/174 (54%)
	42/50 (84%)	104/204 (51%)	146/254 (57%)

Outside of Range (Lowest or Highest Value)[1]

	Community Measures[2]	Population Measures[2]	Total
"Leiorhynchus"-Devonochonetes	11/20 (55%)	25/60 (42%)	36/80 (45%)
Chonetes-Ambocoelia	20/30 (67%)	47/144 (33%)	67/174 (39%)
	31/50 (62%)	72/204 (35%)	103/254 (41%)

1. Low or high ranks are each eguiprobable and rare based upon the randomization model (see Appendix 5.3).
2. See Appendices 5.1 and 5.2 for niche equations, sampling units, and populations.

TABLE 5.5

Breakdown of Table 5.4 Comparisons by Type of Measure and Environment

Community Measures

		"Leiorhynchus"-Devonochonetes						*Chonetes-Ambocoelia*							
Measure[1]	Rank	E1	E2	E3	E4	Total		E1	E2	E3	E4	E5	E6	Total	
8	1-5[2]	+	+	+	+	4		+	+		+	+	+	5	
	96-100[2]					0								0	
11	1-5	+	+			2		+		+	+	+		4	
	96-100				+	1								0	
14	1-5		+	+		2		+	+	+	+			4	
	96-100					0								0	
16	1-5	+		+		2		+		+	+	+		4	
	96-100		+		+	2			+				+	2	
18	1-5	+	+	+	+	4		+	+	+	+	+	+	6	
	96-100					0								0	
	1-5					14								23	
	96-100					3	17/20							2	25/30

Population Measures

		"Leiorhynchus"-Devonochonetes						*Chonetes-Ambocoelia*							
Measure[1]	Rank	E1	E2	E3	E4	Total		E1	E2	E3	E4	E5	E6	Total	
7	1-5	2	3	2	2	9		2	2	1	2	2	2	11	
	96-100			1		1	10/20[3]	1	1		2		2	6	17/48[4]
13	1-5	3	2	3	3	11		5	6	6	5	5	5	32	
	96-100	1	2	2	2	7	18/20	1	2	2	2	1	1	9	41/48
15	1-5	2		1		3		1	1	1	2	2		7	
	96-100		1	1	2	4	7/20	1	1			1	1	4	11/48
	1-5					23								50	
	96-100					12								19	

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units (habitats) grouped as environments, and populations.
2. Rank 1-5 or 96-100 of the Field Data Value in the combined set of 99 Random Generated Data and 1 Field Data Value.
3. *"Leiorhynchus"-Devonochonetes* has five populations for each of four environments or 20 possible comparisons with equivalent Random Generated Data.
4. *Chonetes-Ambocoelia* has eight populations for each of six environments or 48 possible comparisons with equivalent Random Generated Data.

TABLE 5.6

"*Leiorhynchus*"-*Devonochonetes* Field Data Coefficient of Variation Results

Measure[1]	E1	E2	E3	E4	CV	CV Rank
7-1	1.37	0.95	0.96	1.10	17.87%	3
7-2	0	0.32	0.40	0.70	81.04	6
7-3	0.87	1.05	0.99	1.10	9.89	1
7-4	1.46	0.59	0.84	0.45	53.51	5
7-5	0.57	0.16	0.43	0.42	43.29	4
8	0.86	0.62	0.72	0.75	13.39	2
13-1	0.15	0.36	0.39	0.34	35.04	3
13-2	0	0.04	0.07	0.07	73.70	5
13-3	0.80	0.50	0.54	0.44	27.85	2
13-4	0.07	0.19	0.05	0.14	57.32	4
13-5	0.03	0.02	0.06	0.12	78.26	6
14	0.21	0.22	0.22	0.22	2.30	1
15-1	0.83	1.02	1.01	0.94	9.22	2
15-2	0	0.96	1.10	1.11	67.22	6
15-3	1.07	0.97	1.00	0.92	6.33	1
15-4	0.78	1.09	0.96	1.31	21.55	3
15-5	0.27	1.26	0.68	1.34	57.01	5
16	0.59	1.06	0.95	1.12	25.52	4

Average Coefficient of Variation Rank		
	1. *Devonochonetes setigerus*	2.7
	2. *Camarotoechia congregata*	5.7
	3. *"Leiorhynchus" sp.*	1.3
	4. *Ambocoelia umbonata*	4.0
	5. *Mucrospirifer mucronatus*	5.0
	- Community values	2.3

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units, and populations.

TABLE 5.7

***Chonetes-Ambocoelia* Field Data Coefficient of Variation Results**

Measure[1]	E1	E2	E3	E4	E5	E6	CV	CV Rank
7-1	0.70	0.82	0.88	0.35	1.21	0.34	46.59%	7
7-2	0.51	0.76	0.86	0.56	0	0.67	54.06	8
7-3	1.05	0.99	1.00	1.01	0.90	1.00	5.00	1
7-4	0.77	0.82	0.92	1.02	1.41	0.73	26.56	6
7-5	0.64	0.54	0.76	1.04	0.99	0.78	24.53	5
7-6	0.81	0.76	0.71	0.71	0.67	0.68	7.30	2
7-7	0.91	0.68	0.92	0.54	0.84	1.01	21.39	4
7-8	0	0.17	0	0.87	1.22	0.44	111.24	9
8	0.67	0.69	0.76	0.76	0.90	0.71	11.07	3
13-1	0.02	0.04	0.05	0.02	0.01	0.05	54.39	6
13-2	0.14	0.05	0.01	0.03	0	0.01	130.38	8
13-3	0.72	0.65	0.65	0.43	0.86	0.80	21.90	3
13-4	0.14	0.29	0.25	0.19	0.10	0.08	47.77	4
13-5	0.03	0.03	0.03	0.03	0.02	0.02	19.36	2
13-6	0.01	0.03	0.02	0.01	0.04	0.09	90.33	7
13-7	0.02	0.02	0.02	0.06	0.03	0.03	51.64	5
13-8	0	0.01	0	0.33	0.06	0.03	179.43	9
14	0.14	0.14	0.13	0.14	0.14	0.14	2.95	1
15-1	0.98	0.97	1.03	0.97	0.86	0.99	5.88	2
15-2	1.10	0.87	0.98	0.79	0	1.04	50.99	8
15-3	0.97	0.99	1.00	0.99	1.05	1.00	2.68	1
15-4	1.10	1.04	1.00	0.99	.058	1.00	19.61	7
15-5	1.17	1.05	0.90	0.94	1.00	1.01	9.30	3
15-6	0.82	1.02	1.09	1.09	1.20	1.03	12.10	6
15-7	0.97	1.03	0.94	0.77	1.09	0.99	11.27	5
15-8	0	1.09	0	1.05	0.31	1.01	92.14	9
16	0.89	1.01	0.87	0.95	0.76	1.01	10.48	4

Average Coefficient of Variation Rank	Taxon	Value
	1. *Orbiculoidia media*	5.0
	2. *Tropidoleptus*	8.0
	3. *Chonetes cf. lineatus*	1.7
	4. *Ambocoelia umbonata*	5.7
	5. *Cyrtina*	3.3
	6. *Mucrospirifer mucronatus*	5.0
	7. "*Tylothyris*"	4.7
	8. *Sulcoretepora gilberti*	9.0
	- Community values	2.7

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units, and populations.

TABLE 6.1

Direction of Change in Numbers[1]

	from before layer to *Sulcoretepora* layer	from *Sulcoretepora* layer to after layer
1. crinoids	+	-
2. *Sulcoretepora*	+	-
3. other Bryozoans	+	-
4. nuculanas	-	(+)
5. *Chonetes*	-	+
6. immobile Brachiopods (not *Chonetes*)	(-)	(+)
7. low attached Brachiopods	+	+

1. Based on raw numbers, % total of sampling units, and % change for populations and guilds comprising greater than 2% of fossils in sampling units used in this chapter ("other bryozoans" included for comparison to Sulcoretepora purposes) -- see Appendix 6.3 for raw data and Appendix 6.4 for scoring the data.

TABLE 6.2

Parameter Change Effects on Figure 6.1[1]

								Known change before[2]			
								+	-	+	+
								Known change after[2]			
								-	+	+	-
		Effect on Numbers									
		R1	R2	R3	R4	Pr5	Pr6	cri	cho	bra	sul
Where	R1	?	-	+	+	-	+	-	+	-	-
Para-	R2	-	?	-	-	+	-	+	-	+	+
meter	R3	+	-	(-)	(-)	-	(-)	-	+	-	(+)
Change	R4	+	-	(+)	(-)	-	(-)	-	+	(+)	-
Enters	Pr5	-	+	-	-	?	-	+	-	+	+
System	Pr6	+	-	(-)	(-)	-	(-)	-	+	(+)	(+)
	cri	+	-	+	+	-	+	-	+	-	-
	cho	-	+	-	-	+	-	+	-	+	+
	bra	+	-	+	-	-	-	-	+	-	(+)
	sul	+	-	-	+	-	(-)	-	+	(+)	-

1. Assume negative parameter change -- reverse signs give results of positive parameter change.
2. See Table 6.1.

	enter parameter change		Chonetes Turnover Rate prediction
BEFORE	R1	positive	- larger
	R2	negative	(-) larger
	Pr5	negative	- larger
	cri	positive	- larger
	cho	negative	- larger
AFTER	R4	negative	(+) smaller
	sul	negative	(+) smaller

TABLE 6.3

***Chonetes* Measurement Evaluation**[1]

	Lebanon Center Road below	Sulco.	above	Geer Road below	Sulco.	above	Deep Spring Road below	Sulco.	above
Average Size (mm.)	5.9	6.3	6.1	6.0	6.5	6.4	6.1	6.2	6.3
Number	20	30	27	90	52	82	40	36	26
t	0.86	0.35		1.28	0.28		0.22	X	
P-value (one tail)	<0.20	<0.37		<0.11	<0.39		<0.42	X	

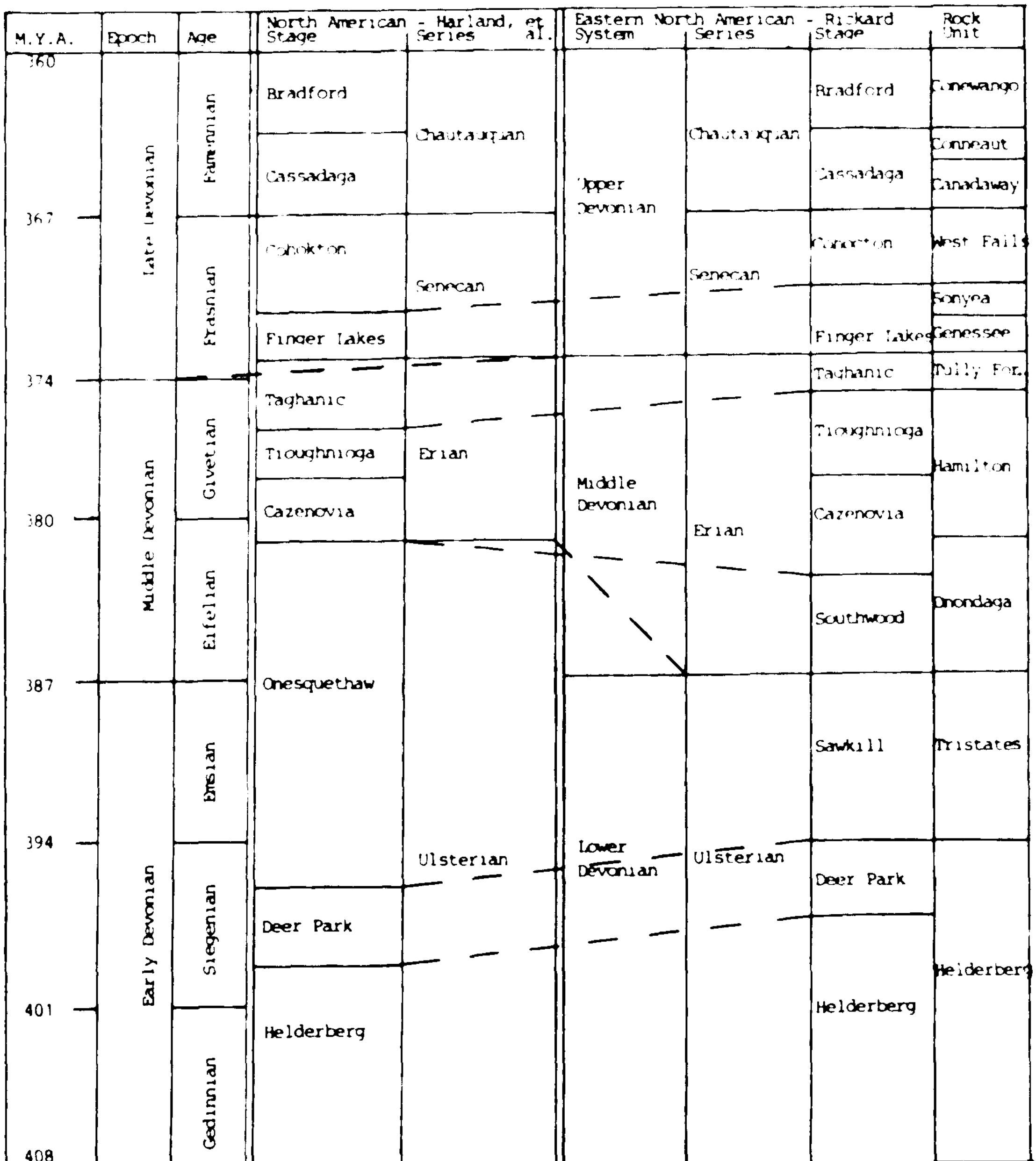
X = Results reverse of prediction, one-tailed T-test inappropriate since <u>directionality</u> has been predicted.

<u>TOTAL</u>	below	Sulco. layer	above
Average Size (mm.)	6.0+/-1.9 SD	6.4+/-2.3 SD	6.3+/-2.0 SD
Number	150	118	135
t	1.40*	0.18	
P-value (one tail)	<0.09	<0.43	

1. Based on measures given in Appendix 6.6.

FIGURE [illegible] Hamilton Group in the Devonian Period

(sources: Rickard, 1975 and Harland, et al., 1982)



Age estimates: error function from 6 M.A. at Devonian boundaries up to 14 M.A. for certain Ages.

FIGURE 1.2 Hamilton Group in New York

(after Eldredge, 1972; Baird, 1979; Grasso, 1986, and Brett, Speyer and Baird, 1986)

Stage	Western New York	Central New York	Formation
Taghanic		Tully, W. Brook	Moscow
		Tully, Apulia	
	Leicester		
Upper Tioughnioga			
	Windom	Windom / Cooperstown	
	Kashong	Kashong / Cooperstown	
??	Menteth	Portland Point	
Middle Tioughnioga	Deep Run		
	Tichenor		
	Jaycox	"King Ferry"	Ludlowville
	Wanakah		
	Ledyard	Otisco	
Lower Tioughnioga	Centerfield	Stone Mill	
Upper Cazenovia	Levanna	Butternut	Skaneateles
		Pompey	
		Delphi Station	
	Stafford	Mottville	
Lower Cazenovia	Oatka Creek	Cardiff (incl. Solsville) 1. 2. 3.	Marcellus: 1. Pecksport 2. Solsville 3. Bridgewater
		Chittenango	
	Seneca	Cherry Valley	
		Union Springs	
		Seneca	
	Moorehouse	Moorehouse	

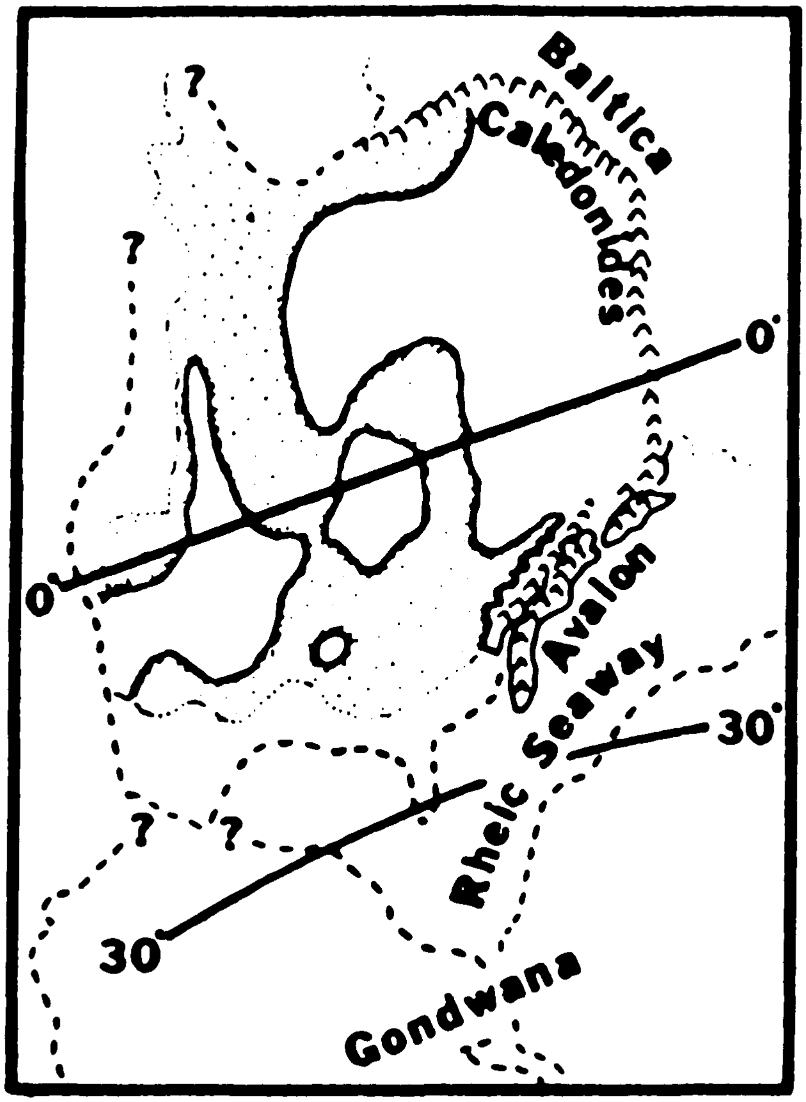


FIGURE 1.3 Paleogeography of North America during Middle Devonian (Givetian) time

(this is figure 1.a from Brett, Speyer and Baird, 1986)
(stippled area represents epeiric seaway)
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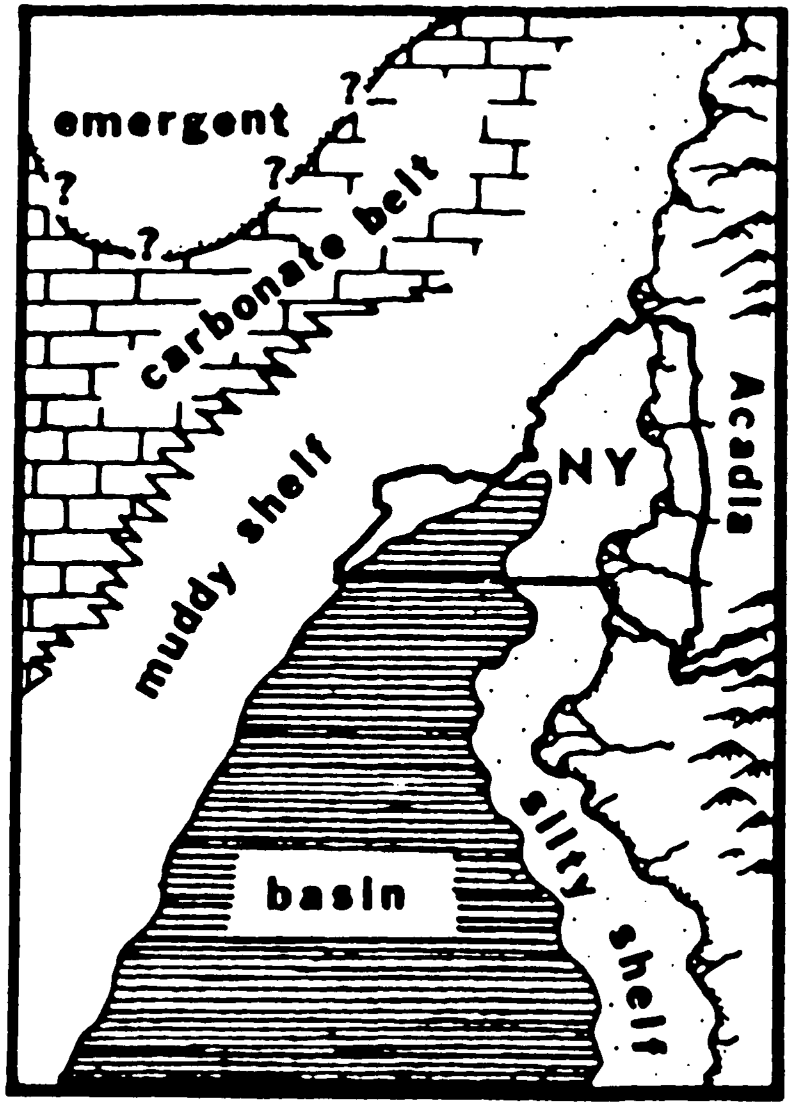

FIGURE 1.4 Northeast North America during Middle Devonian (Givetian) time
(this is figure 1.b from Brett, Speyer and Baird, 1986)
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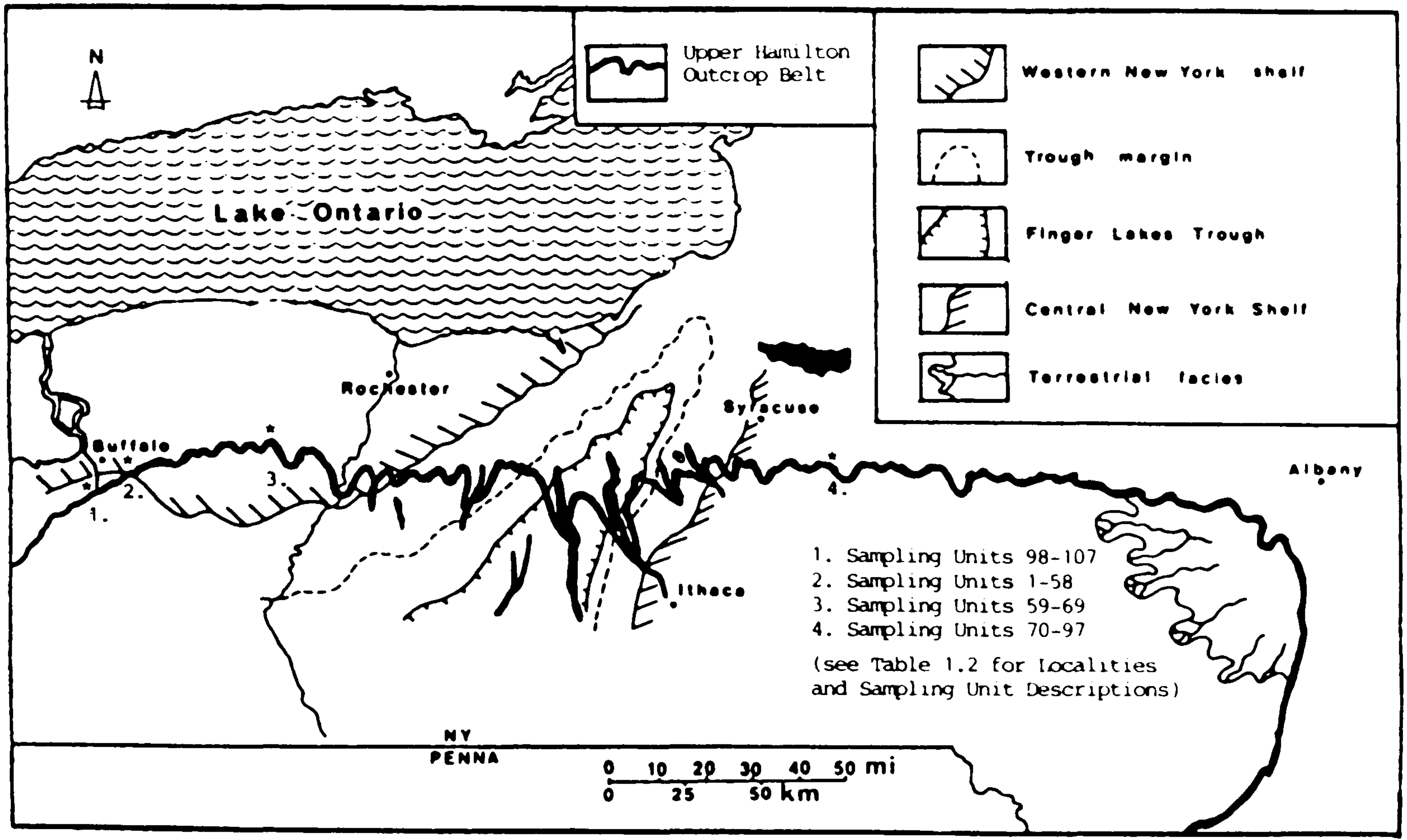

FIGURE 1.5 Sampling Units Located in the Upper Hamilton Outcrop Belt

(adapted from Savarese, Gray and Brett - Figure 1, 1986)

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FIGURE 4.1

Chenango Valley - Windom Member Sample Unit Correlation

	BRADLEY BROOK (SOULE ROAD)	GEER ROAD	LEBANON CENTER ROAD	DEEP SPRING ROAD
7-8 m.	calcareous fossiliferous layer (6-10cm.)	not seen	hard fossiliferous layer (variable width)	?
5-5.5 m.	shale/sandstone bedding plane (2-5cm.)	same (4-5cm.)	same (2-5cm.)	same (2-6cm.)
	?	*Sulcoretepora* layer (8-10cm.)	same	same
4-4.5 m.	?	coquina layer	same	same
0m.	phosphate nodule plane	same	same	?

▭ = sample location

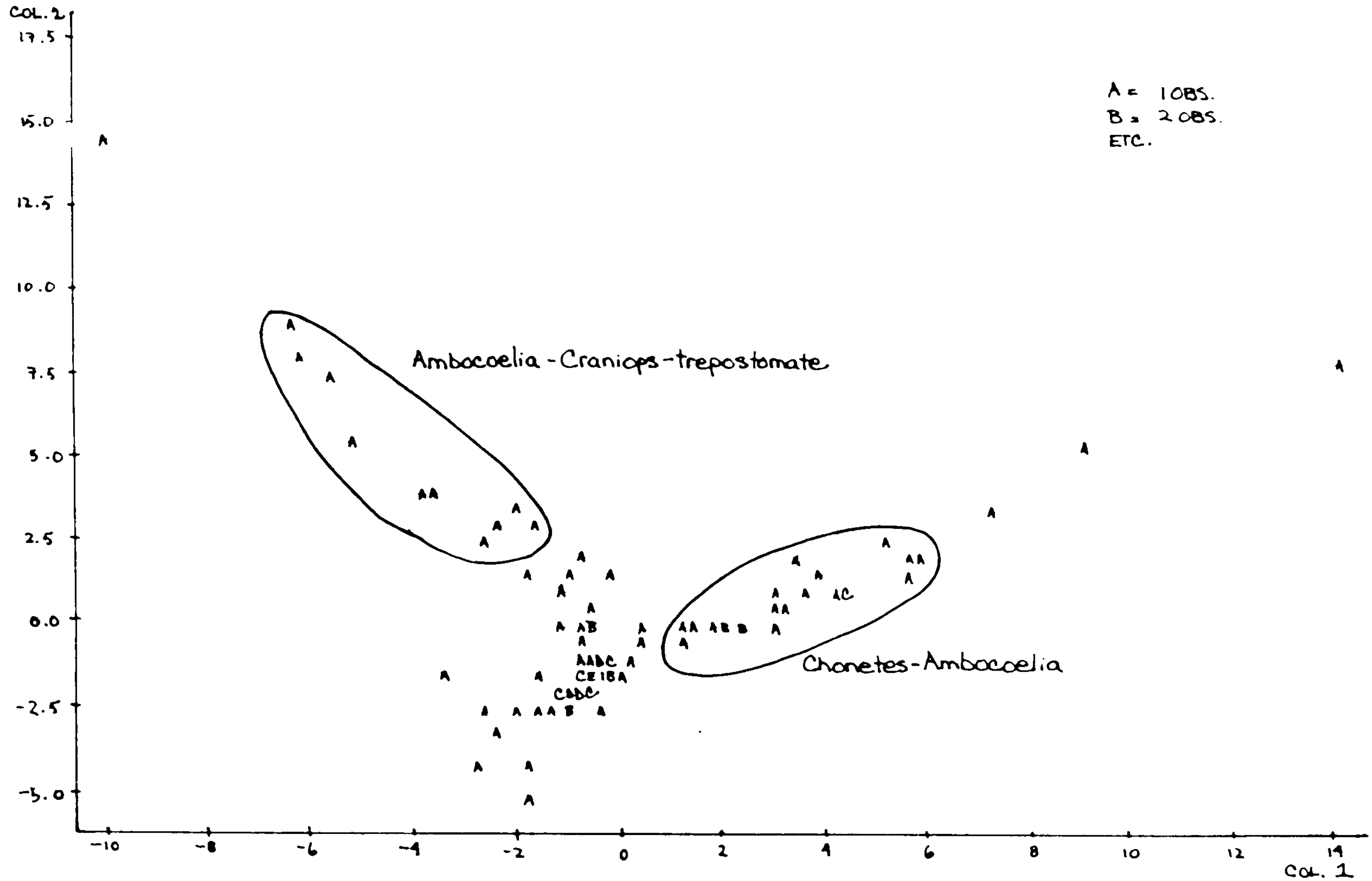


FIGURE 4.2

Principal Components Analysis (Correlation) – PC1 X PC2 Equal Rock Volume Abundance

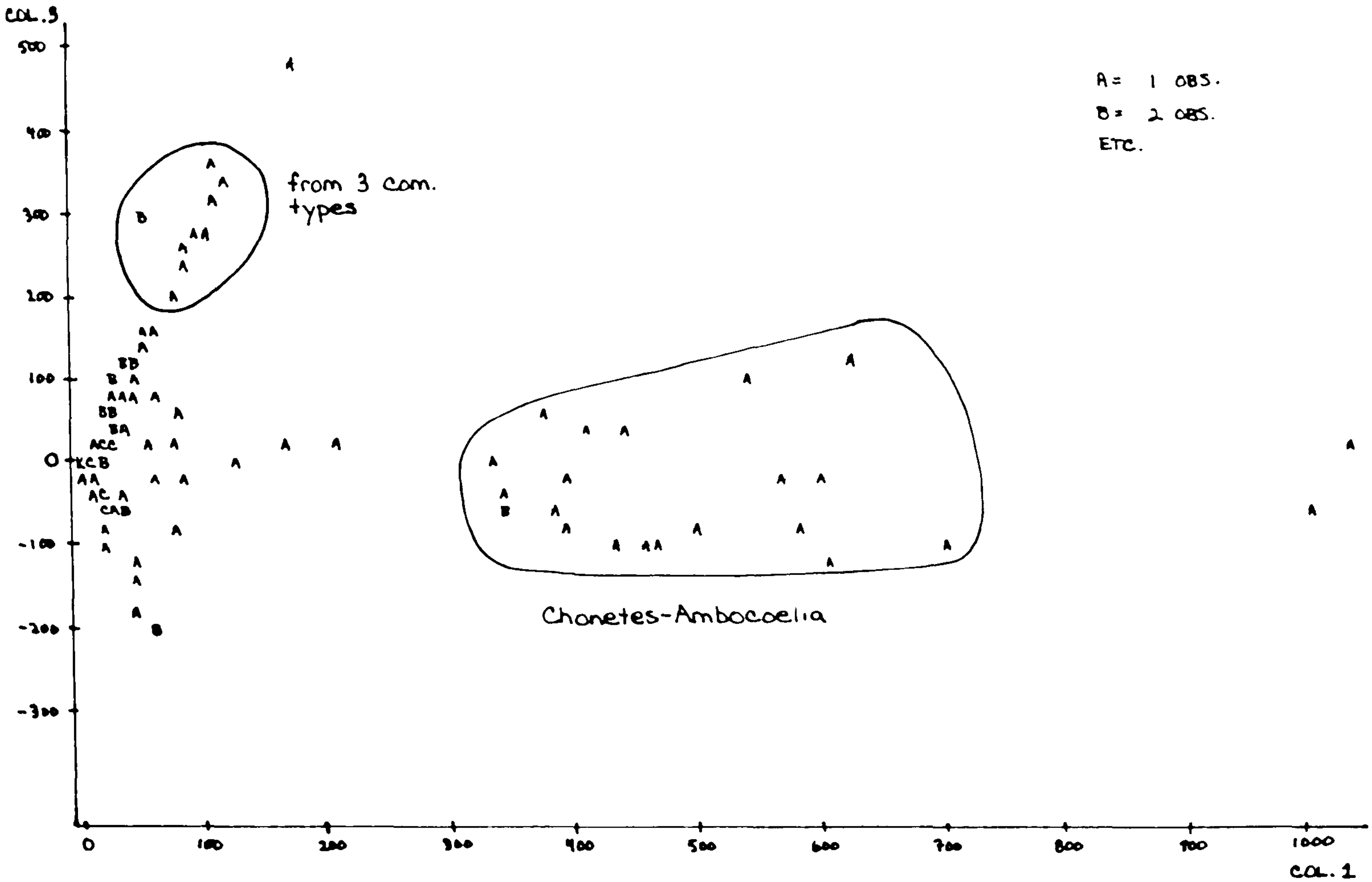


FIGURE 4.3

Principal Components Analysis (Covariance, No Mean Correction) – PC1 X PC3
Equal Rock Volume Abundance

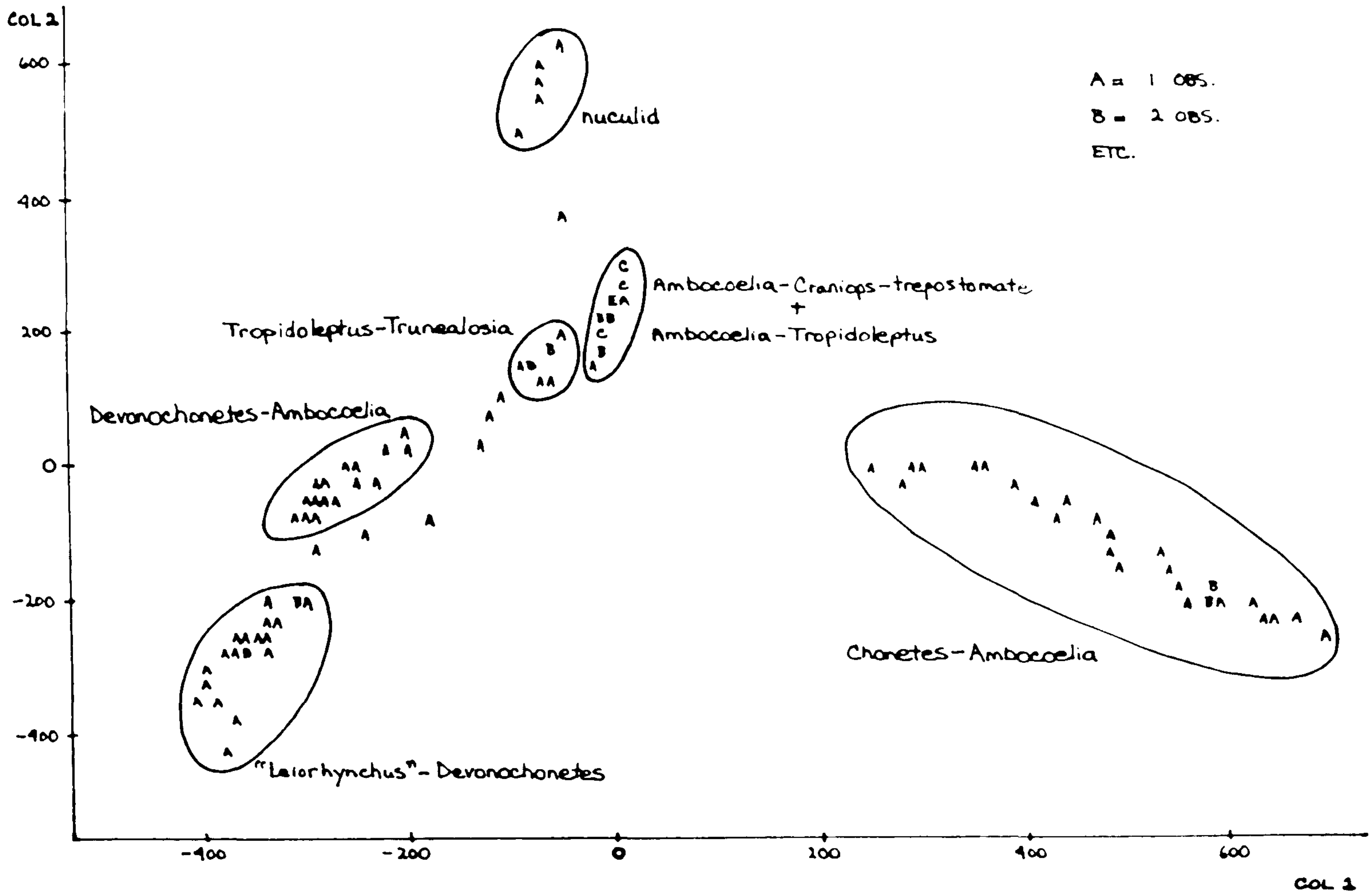
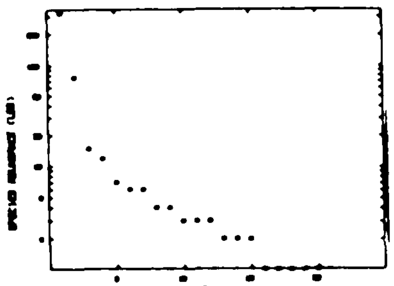


FIGURE 4.4

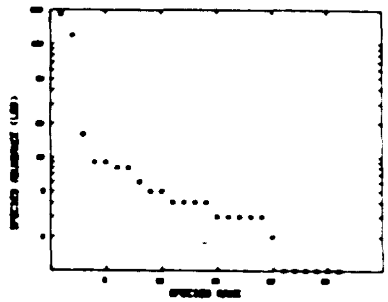
Principal Components Analysis (Covariance) – PC1 X PC2 Percentage Abundance

FIGURE 4.5

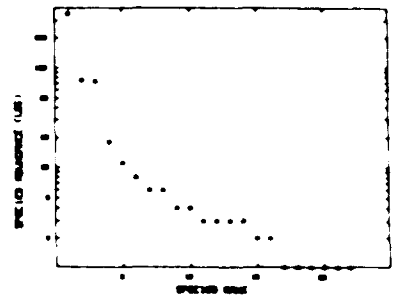
Dominance Diversity Curves



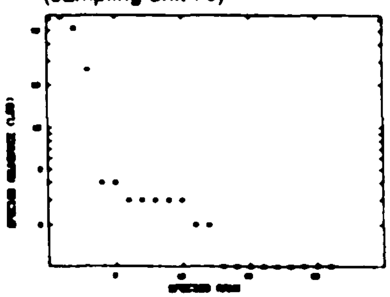
Chonetes-Ambocoelia (sampling unit 70)



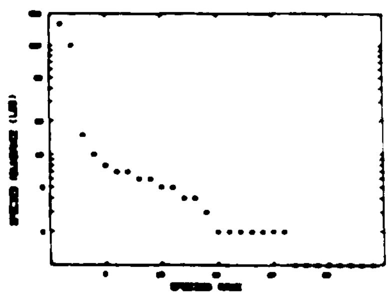
Chonetes-Ambocoelia (s.u. 71)



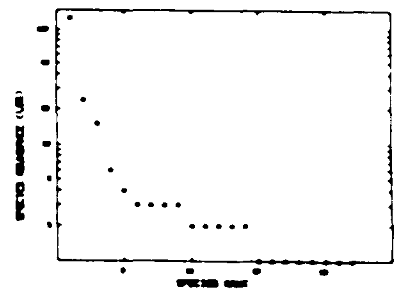
Chonetes-Ambocoelia (s.u. 72)



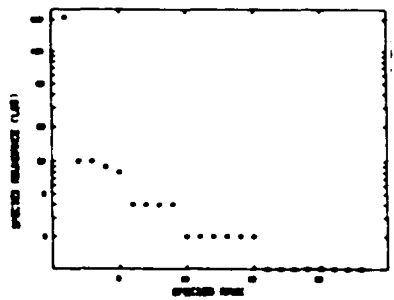
Chonetes-Ambocoelia (s.u. 81)



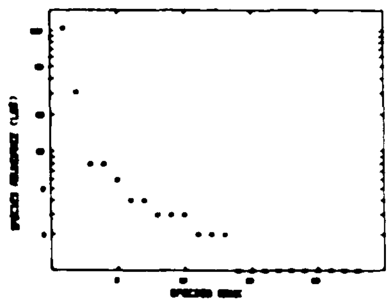
Chonetes-Ambocoelia (s.u. 77)



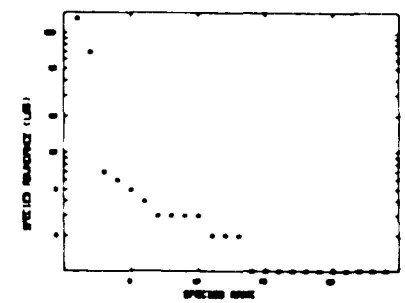
Chonetes-Ambocoelia (s.u. 75)



Chonetes-Ambocoelia (s.u. 95)



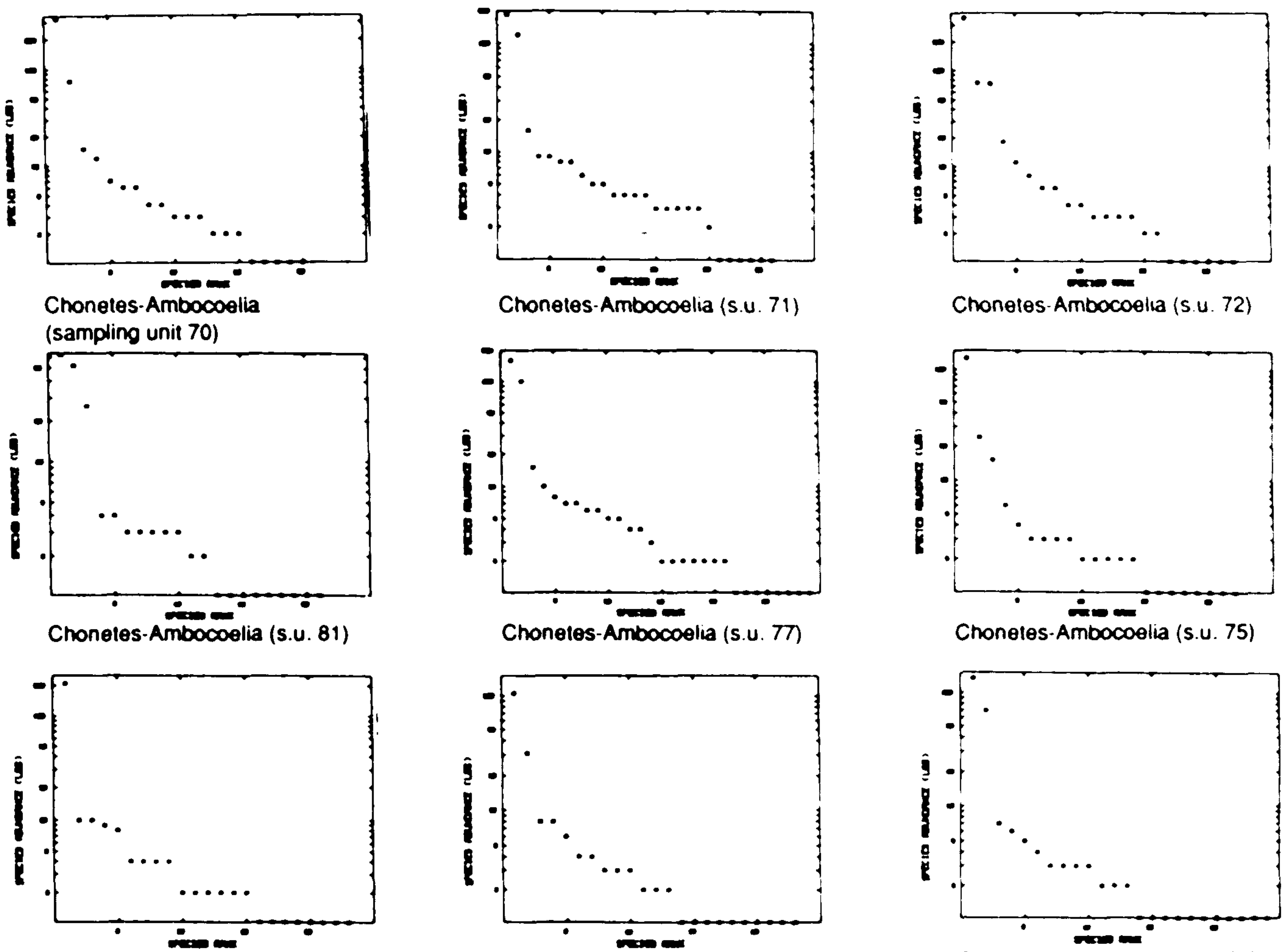
Chonetes-Ambocoelia (s.u. 93)



Chonetes-Ambocoelia (s.u. 88)

FIGURE 4.5

Dominance Diversity Curves



Chonetes-Ambocoelia (sampling unit 70)

Chonetes-Ambocoelia (s.u. 71)

Chonetes-Ambocoelia (s.u. 72)

Chonetes-Ambocoelia (s.u. 81)

Chonetes-Ambocoelia (s.u. 77)

Chonetes-Ambocoelia (s.u. 75)

Chonetes-Ambocoelia (s.u. 95)

Chonetes-Ambocoelia (s.u. 93)

Chonetes-Ambocoelia (s.u. 88)

FIGURE 4.6

Hamilton Fauna: Trophic-Substratum-Mobility for Species Included in this Study[1]
(modified after Bowen, Rhoads, and McAlester, 1974)

Feeding Type	Epifaunal: Unattached: Immobile	Epifaunal: Unattached: Mobile	Epifaunal: Attached: High-Mid.	Epifaunal: Attached: Low	Infaunal: Immobile	Infaunal: Mobile	Swim
Carnivore	121?, 122-124	130, 131	x	x	x	x	(macro.) 114-119, 126?
Grazer +/or Scavenger	x	92-104 108, 109	x	x	x	x	x
Deposit +/or Scavenger	x	110-112, 125?, 132?	x	x	x	35-52	x
Suspension	5-19, 22, 27-29, 31, 33, 120, 127?	128?, 129?	113	2-4, 21, 23, 24?, 25, 26, 30, 32, 34, 53-65, 76 78-91	1, 66-69	70-75, 77	?
Coprophagus?	x	x	105-107?	x	x	x	x

1. See Table 1.4 for species names corresponding to identifying numbers used in this table.

FIGURE 4.7a

Nuculid Community Type: Trophic-Substratum-Mobility Groups

Feeding Type	Epifaunal Unattached Immobile	Epifaunal Unattached Mobile	Epifaunal Attached Hi.-Mid.	Epifaunal Attached Low	Infaunal Immobile	Infaunal Mobile	Swim
Carnivore	O	P	X	X	X	X	P
Graz./Scav.	X	1.5	X	X	X	X	X
Dep./Scav.	X	O	X	X	X	90.7	X
Suspension	2.0	O	O	4.4	0.9	0.2	?

O = not found
P = present but not counted
Number = percent of counted only

FIGURE 4.7b

Ambocoelia-Tropidoleptus Community Type: Trophic-Substratum-Mobility Groups

Feeding Type	Epifaunal Unattached Immobile	Epifaunal Unattached Mobile	Epifaunal Attached Hi.-Mid.	Epifaunal Attached Low	Infaunal Immobile	Infaunal Mobile	Swim
Carnivore	P	P	X	X	X	X	P
Graz./Scav.	X	3.0	X	X	X	X	X
Dep./Scav.	X	1.4	X	X	X	7.8	X
Suspension	32.6	P	P	54.3	0.6	0.1	?

O = not found
P = present but not counted
Number = percent of counted only

FIGURE 4.7c

Ambocoelia-Craniops-trepostomate Community Type: Trophic-Substratum-Mobility Groups

Feeding Type	Epifaunal Unattached Immobile	Epifaunal Unattached Mobile	Epifaunal Attached Hi.-Mid.	Epifaunal Attached Low	Infaunal Immobile	Infaunal Mobile	Swim
Carnivore	P	P	X	X	X	X	P
Graz./Scav.	X	7.2	X	X	X	X	X
Dep./Scav.	X	4.6	X	X	X	4.7	X
Suspension	34.0	P	P	46.3	1.6	0.8	?

O = not found
P = present but not counted
Number = percent of counted only

FIGURE 4.7d

Tropidoleptus-Truncalosia Community Type: Trophic-Substratum-Mobility Groups

Feeding Type	Epifaunal Unattached Immobile	Epifaunal Unattached Mobile	Epifaunal Attached Hi.-Mid.	Epifaunal Attached Low	Infaunal Immobile	Infaunal Mobile	Swim
Carnivore	P	P	X	X	X	X	P
Graz./Scav.	X	2.6	X	X	X	X	X
Dep./Scav.	X	5.6	X	X	X	1.4	X
Suspension	70.5	O	P	19.1	0.4	0.2	?

O = not found
P = present but not counted
Number = percent of counted only

FIGURE 4.7e

Devonochonetes-Ambocoelia Community Type: Trophic-Substratum-Mobility Groups

Feeding Type	Epifaunal				Infaunal		Swim
	Unattached		Attached				
	Immobile	Mobile	Hi.-Mid.	Low	Immobile	Mobile	
Carnivore	P	P	X	X	X	X	P
Graz./Scav.	X	2.7	X	X	X	X	X
Dep./Scav.	X	1.8	X	X	X	0.5	X
Suspension	66.2	O	P	28.4	0.4	<0.1	?

O = not found
P = present but not counted
Number = percent of counted only

FIGURE 4.7f

"Leiorhynchus"-Devonochonetes Community Type: Trophic-Substratum-Mobility Groups

Feeding Type	Epifaunal				Infaunal		Swim
	Unattached		Attached				
	Immobile	Mobile	Hi.-Mid.	Low	Immobile	Mobile	
Carnivore	P	P	X	X	X	X	P
Graz./Scav.	X	1.2	X	X	X	X	X
Dep./Scav.	X	1.2	X	X	X	0.5	X
Suspension	39.0	O	P	57.9	0.4	<0.1	?

O = not found
P = present but not counted
Number = percent of counted only

FIGURE 4.7g

Chonetes-Ambocoelia Community Type: Trophic-Substratum-Mobility Groups

Feeding Type	Epifaunal Unattached Immobile	Epifaunal Unattached Mobile	Epifaunal Attached Hi.-Mid.	Epifaunal Attached Low	Infaunal Immobile	Infaunal Mobile	Swim
Carnivore	O	O	X	X	X	X	P
Graz./Scav.	X	0.5	X	X	X	X	X
Dep./Scav.	X	0.9	X	X	X	3.0	X
Suspension	69.2	P	P	25.1	1.4	0.1	?

O = not found
P = present but not counted
Number = percent of counted only

FIGURE 4.8

Paleoecological Model Relating Ludlowville Biofacies to Inferred Gradients of Depth-Related Parameters and Turbidity and/or Sedimentation Rates

(figure 5 -- Brett, Baird, and Miller, 1986)
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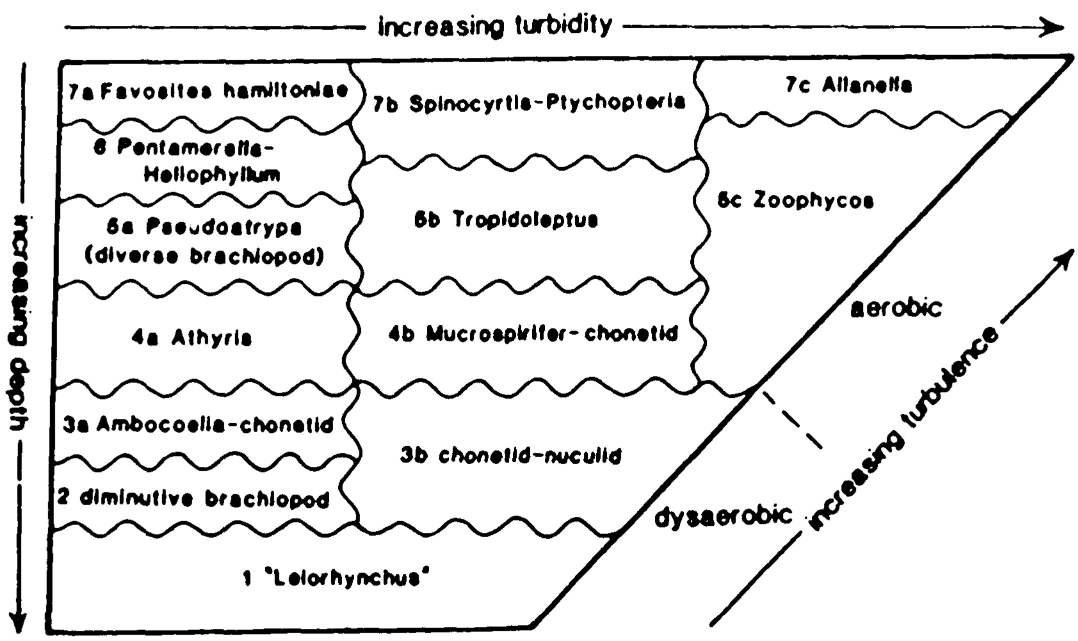


FIGURE 5.1

The hierarchical grouping of sampling units according to the method used in this chapter.

The procedure starts with the identification of these sampling units as part or all of a community type. (Because of the requirements of the method, not all sampling units of a community type are necessarily appropriate for use with this method.)

In translating this neoecological method to paleoecology, some clarification of terminology may be useful. This is because of the different time frames involved: in neoecology, a season or a few years, while in paleoecology it may be from a few thousands to hundreds of thousands of years. The underlined terms are those used by Lane, Lauff and Levins (1975). In neoecology, the total sample is considered to be of a community, while in paleoecology it is more appropriate to consider the sample as of a community type. The environment grouping in neoecology is best thought of in paleoecology as a community or part of a community type depending upon the time and geographic distance involved. A population in neoecology is more appropriately regarded as a lineage in paleoecology.

Habitat: an individual sampling unit in this study.

Environment: a group of sampling units (Habitats) from the same time facies and/or a time-locational grouping in a series of sampling units. Thus, Habitats 84, 91, and 97 from the *Chonetes-Ambocoelia* community type are from the same layer in nearby localities, (or, these Habitats might have represented a series of sampling units from one locale which is found to be "repeated" in earlier and/or later sampling regimes. Repeated means they are found to be part of a community type (see text and Chapter 4 for methods used in this study to identify community types).)

Community: a group of Environments from the same community type.

Neoecology	**Paleoecology**
community	community type
environment	community or part of a community type
population	lineage
habitat	sampling unit

Figure 5.1 continued.

Community (community type) -- *Chonetes-Ambocoelia*[1]

	Geer Road	Lebanon Center Rd.	Deep Spring Road	Bradley Brook
E6	H72, H78	H74, H85	H76, H92	H70
E5	H73, H79	H75, H86	H77	H71
E4	H80	H88	H93	
E3	H81	H89	H94	
E2	H82	H90	H95	
E1	H84	H91	H97	

E = Environment (community) -- layer in this example.
H = Habitat -- sampling unit in this example.

1. See Appendix 5.2 for full population data for each habitat (sampling unit) for this example.

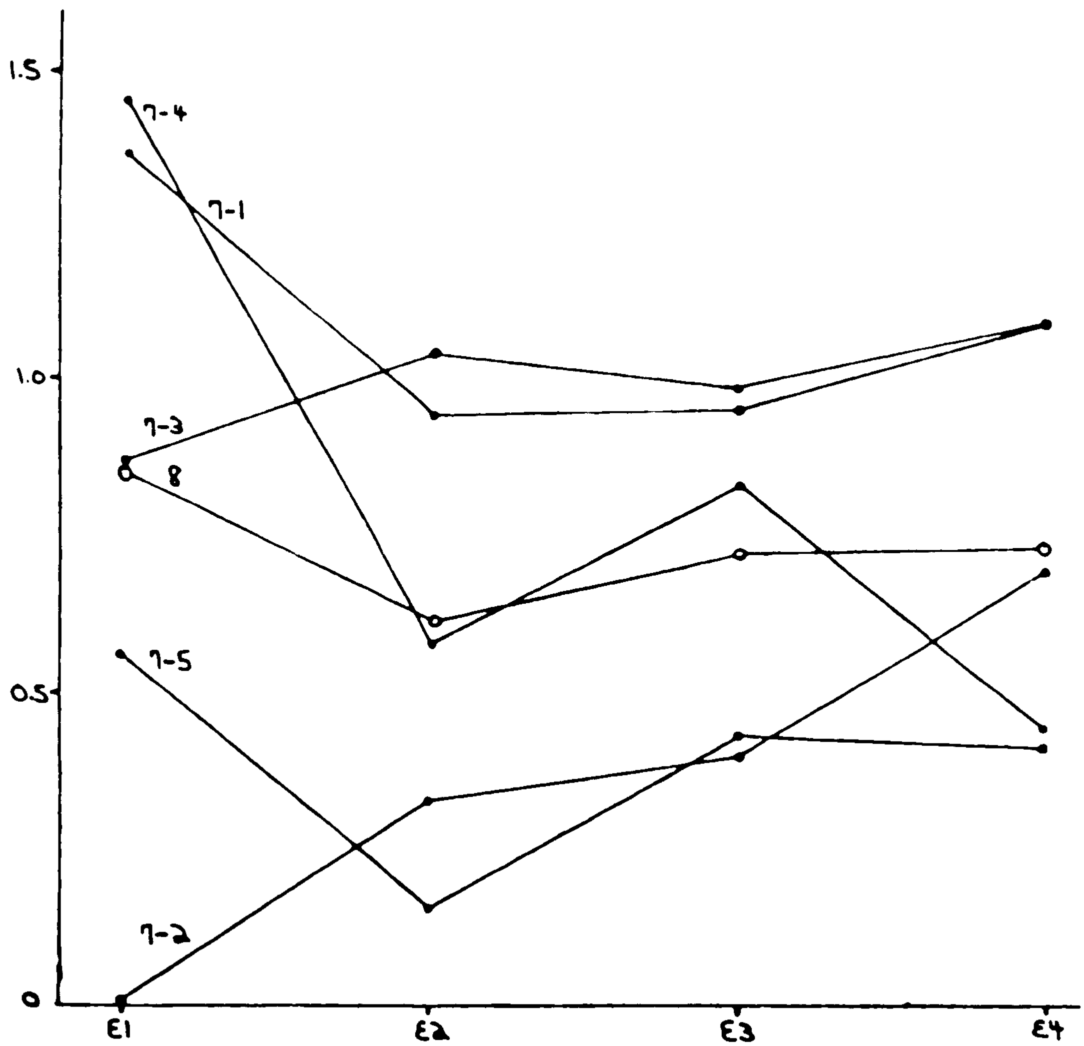


FIGURE 5.2a

Graph of values of relative niche breadth for populations and community for *"Leiorhynchus"-Devonochonetes*[1]

7-1. *Devonochonetes setigerus*
7-2. *Camarotoechia congregata*
7-3. *"Leiorhynchus" sp.*
7-4. *Ambocoelia umbonata*
7-5. *Mucrospirifer mucronatus*
8. Community value

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units (grouped as habitats (E)), and populations.

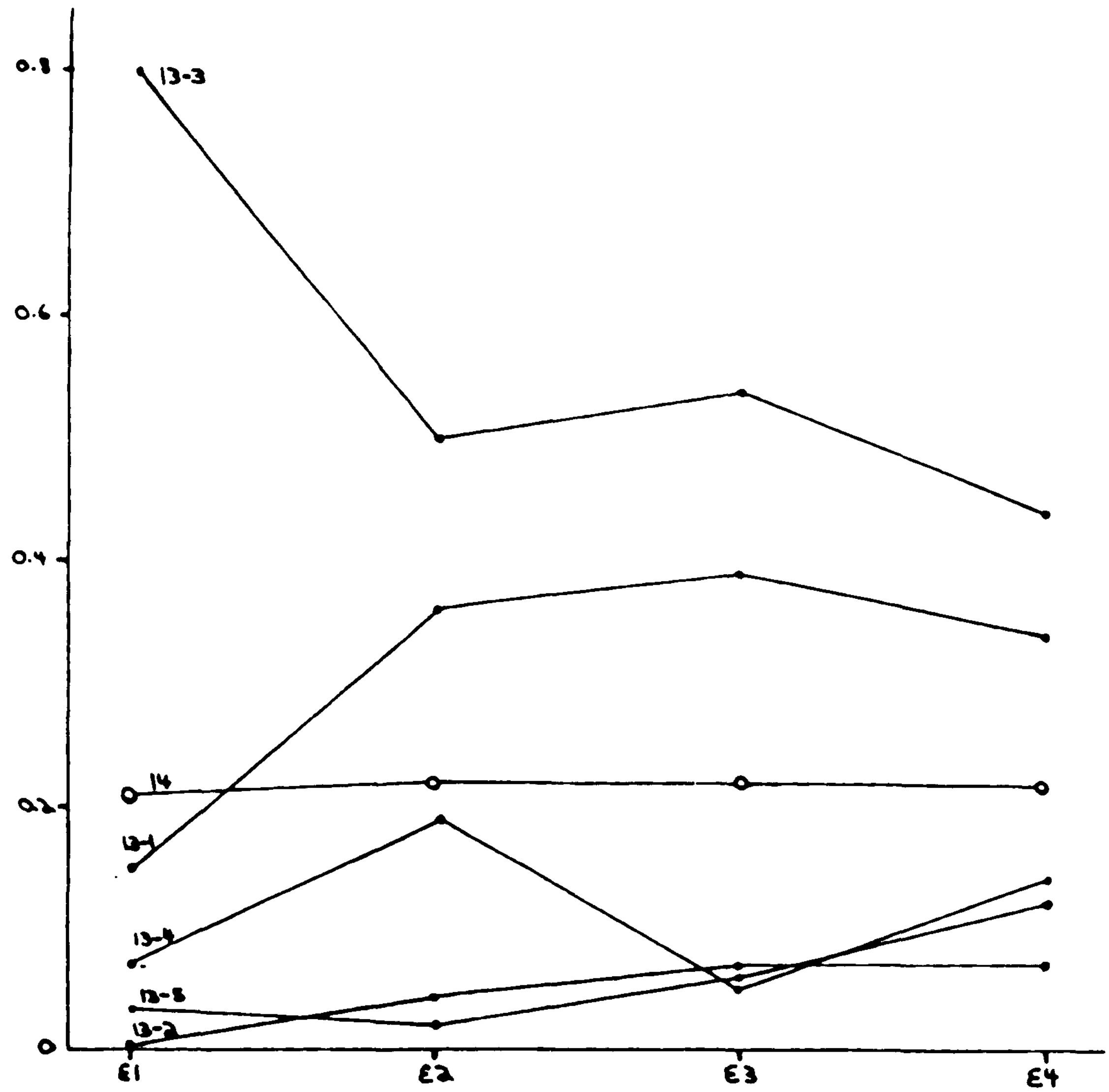


FIGURE 5.2b

Graph of values of co-occurrence success ratio for populations and community for *"Leiorhynchus"-Devonochonetes*[1]

13-1. *Devonochonetes setigerus*
13-2. *Camarotoechia congregata*
13-3. *"Leiorhynchus" sp.*
13-4. *Ambocoelia umbonata*
13-5. *Mucrospirifer mucronatus*
14. Community value

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units (grouped as habitats (E)), and populations.

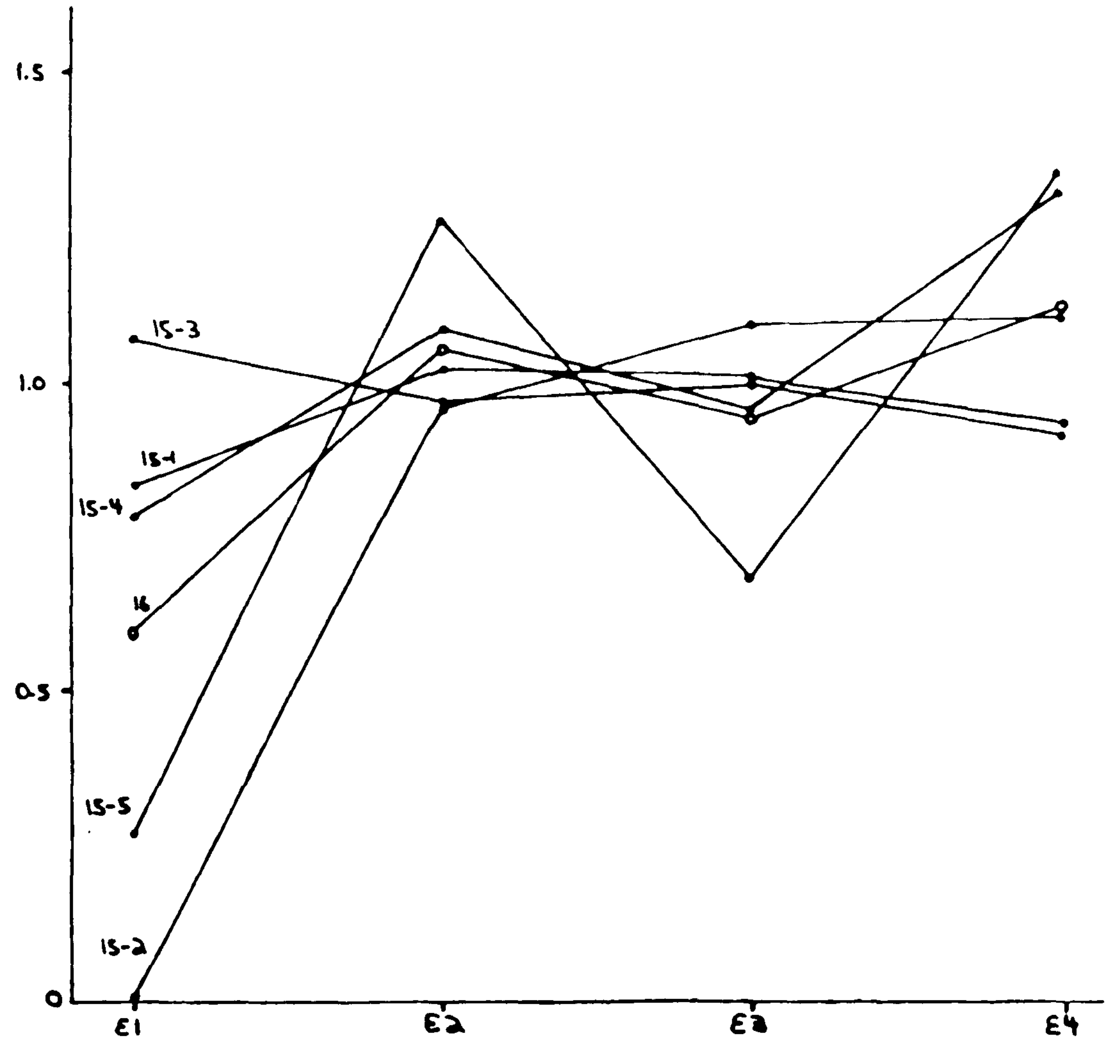


FIGURE 5.2c

Graph of values of utilization efficiency ratio for populations and community for *"Leiorhynchus"-Devonochonetes*[1]

15-1. *Devonochonetes setigerus*
15-2. *Camarotoechia congregata*
15-3. *"Leiorhynchus" sp.*
15-4. *Ambocoelia umbonata*
15-5. *Mucrospirifer mucronatus*
16. Community value

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units (grouped as habitats (E)), and populations.

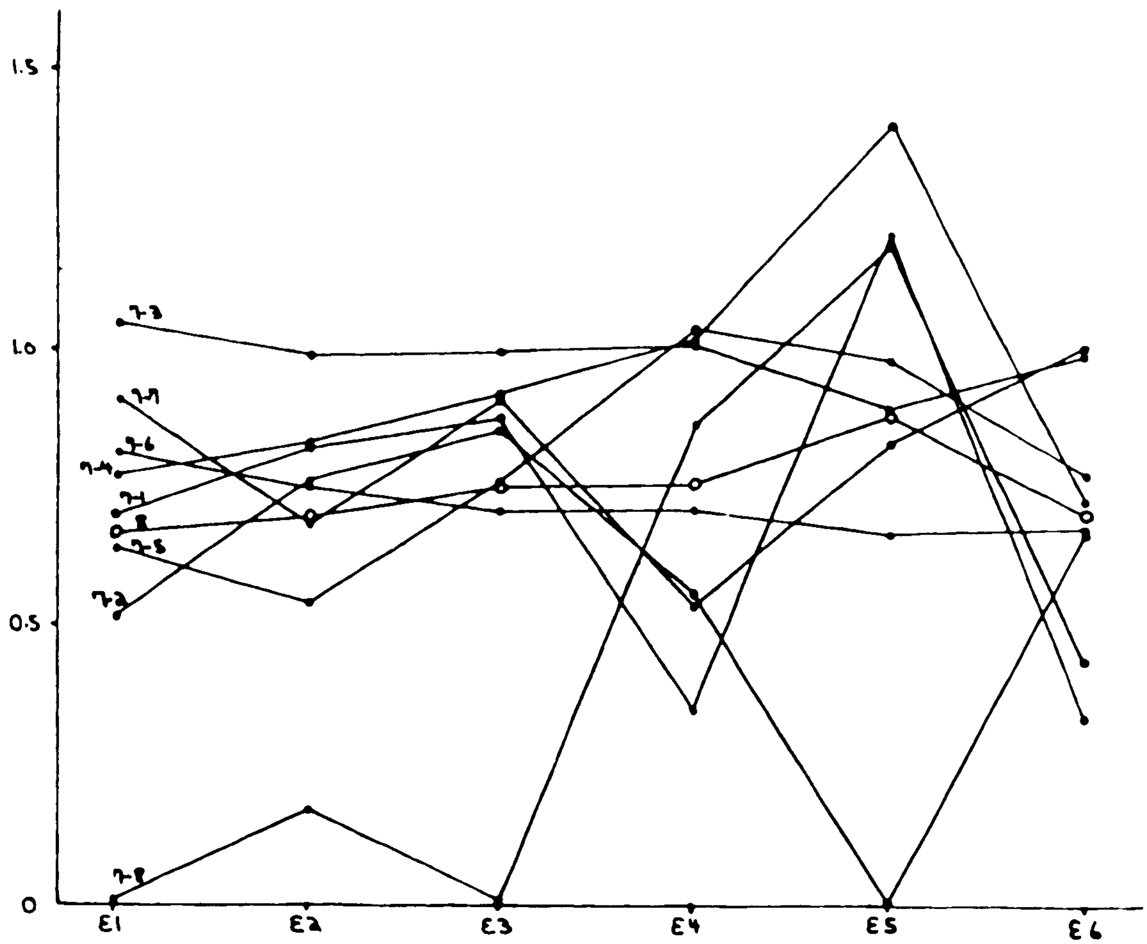


FIGURE 5.3a

Graph of values of relative niche breadth for populations and community for *Chonetes-Ambocoelia*[1]

7-1.	*Orbiculoidea media*	7-5.	*Cyrtina*
7-2.	*Tropidoleptus*	7-6.	*Mucrospirifer mucronatus*
7-3.	*Chonetes cf. lineatus*	7-7.	*"Tylothyris"*
7-4.	*Ambocoelia umbonata*	7-8.	*Sulcoretepora gilberti*
8.	Community value		

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units (grouped as habitats (E)), and populations.

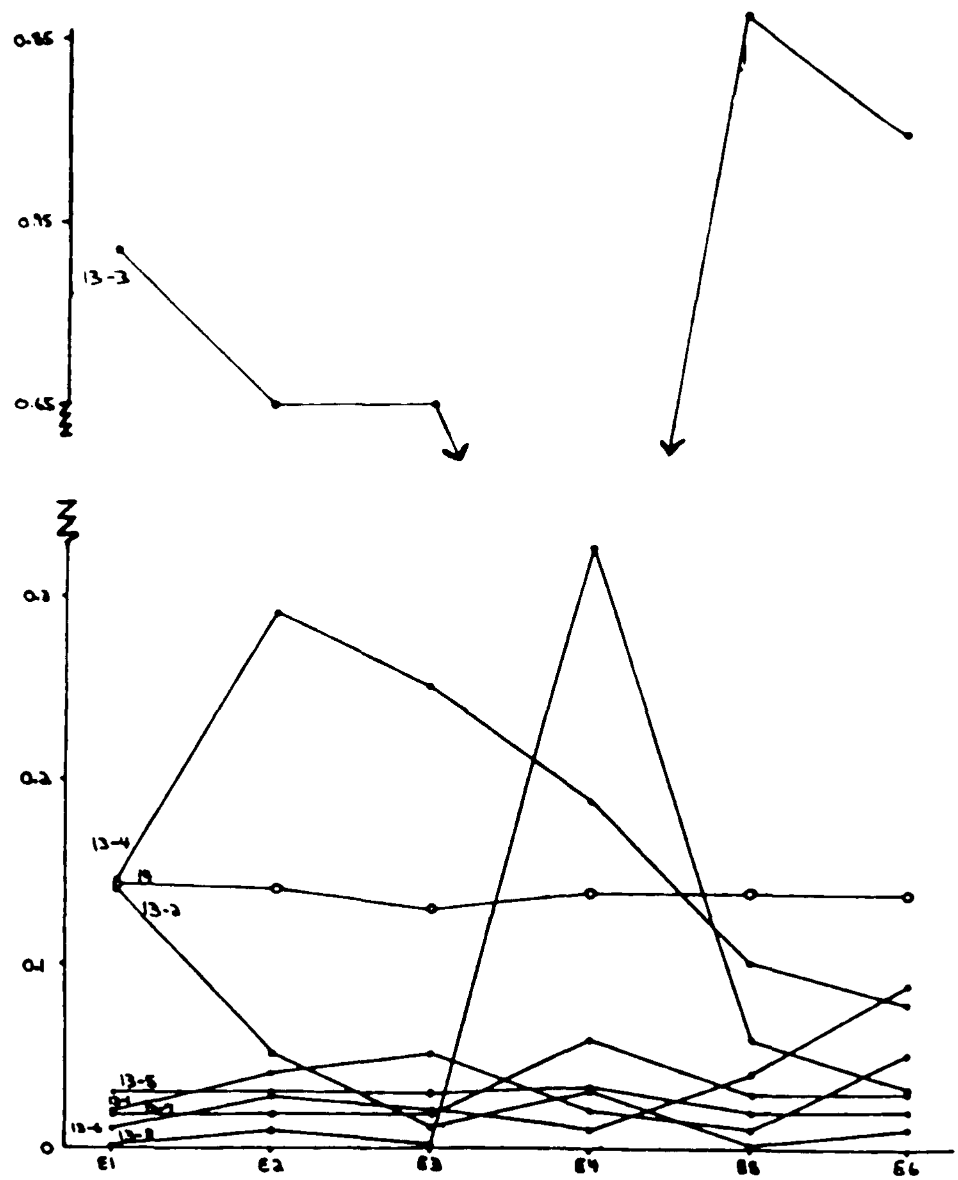


FIGURE 5.3b

Graph of values of co-occurrence success ratio for populations and community for *Chonetes-Ambocoelia*[1]

13-1.	*Orbiculoidea media*	13-5.	*Cyrtina*
13-2.	*Tropidoleptus*	13-6.	*Mucrospirifer mucronatus*
13-3.	*Chonetes cf. lineatus*	13-7.	*"Tylothyris"*
13-4.	*Ambocoelia umbonata*	13-8.	*Sulcoretepora gilberti*
14.	Community value		

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units (grouped as habitats (E)), and populations.

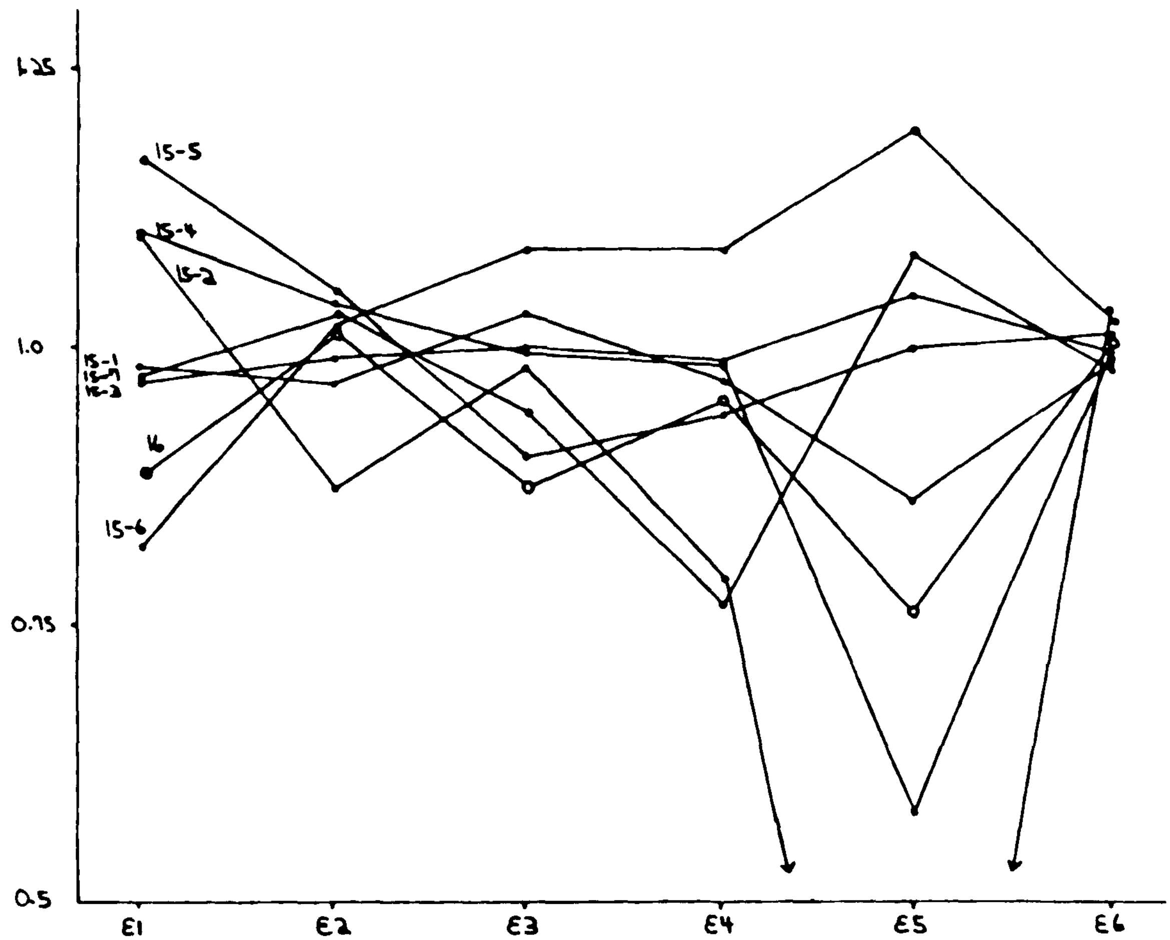


FIGURE 5.3c

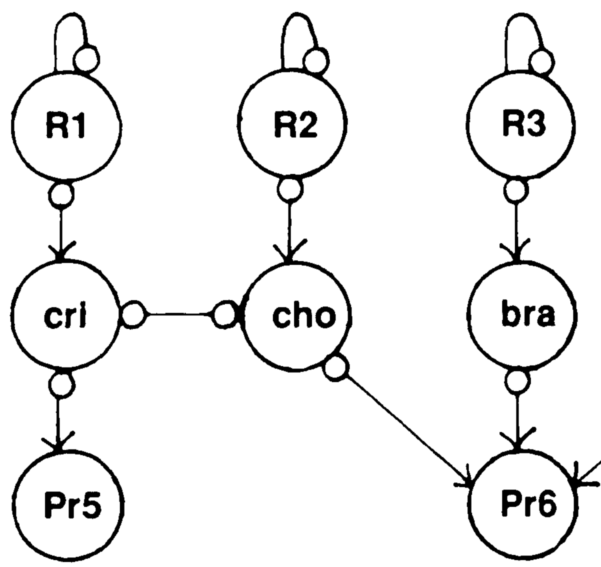
Graph of values of utilization efficiency ratio for populations and community for *Chonetes-Ambocoelia*[1]

15-1.	*Orbiculoidea media*	15-5.	*Cyrtina*
15-2.	*Tropidoleptus*	15-6.	*Mucrospirifer mucronatus*
15-3.	*Chonetes cf. lineatus*	15-7.	*"Tylothyris"*
15-4.	*Ambocoelia umbonata*	15-8.	*Sulcoretepora gilberti*
16.	Community value		

1. See Appendices 5.1 and 5.2 for niche equations (measures), sampling units (grouped as habitats (E)), and populations.

FIGURE 6.1

Digraph Which Under Various Parameter Change Effects Will Give the Observed Changes in Numbers (Signs) for the Most Abundant Populations of the Sampling Units Discussed in Chapter 6



R1-R4	resources: combination of spatial and nutritional factors
Pr5-Pr6	"predators"
cri	crinoids
cho	*Chonetes*
bra	attached Brachiopods
sul	*Sulcoretepora*

APPENDIX 4.1

Equal Rock Volume Adjustments

When comparing samples based upon different rock volumes (e.g., for a full 107 sampling unit comparison), adjustments to the raw data due to different rock volumes were necessary. McCollum (1980) sampled from 1.25 x 10^5 cm^3 sections; Brett from an average of 0.47 x 10^5 cm^3 sections (range of 0.26 x 10^5 cm^3 to 0.82 x 10^5 cm^3); and Pilette from 0.02 x 10^5 cm^3 sections (each excepting bedding planes). The rock volume ratios are roughly 60:20:1.

McCollum and Brett each sampled fossils as part of studies primarily aimed at paleoenvironmental analysis. Their 2.7:1 rock volume ratio is close to their average fossil count ratio (excluding bedding plane sampling units) of 2.6:1. On this basis, I multiplied the Brett counts by a factor of 3 when Brett and McCollum data were evaluated together in an Equal Rock Volume analysis.

The McCollum and Pilette rock ratio is 60:1. McCollum (personal communication) did not go through the exposed rock on as fine a basis as I did. Aiming at an overall environmental analysis, McCollum counted only observable fauna in her large rock volume sampling units. Though looking for ostracodes and other small macrofauna, exposed chunks of rocks were not further broken down. In contrast, I passed all of the rock I exposed through my fingers. I concentrated on getting exact counts of brachiopods, pelecypods, bryozoans, gastropods, and trilobites for a community-focused study.

To get a better sense of the adjustment factor needed between McCollum and myself, I compared our bedding plane sampling unit ratios based upon equal rock areas. These are 1:7.3. But, again, McCollum probably undercounted. On the basis of these considerations, I decided to multiply my sampling unit counts by a factor of 3 when McCollum's and my data were evaluated together in an Equal Rock Volume analysis. This gives a faunal ratio of 1:1.5.

Having made these adjustments, no further adjustment was seen as necessary (and none was suggested when looking at the data) for comparisons of Brett's and my data in an Equal Rock Volume analysis. This gives a faunal ratio of 1:1.3.

There is much room for the imagination here. However, it does not seem unreasonable to assume the possibility that the Chenango sampling units used in this study have a slightly higher density fauna than the Alden, Elma, and western New York Windom sampling units used in this study, and that these last, because of different investigative intent (paleoenvironmental rather than paleocommunity) were undercounted originally.

APPENDIX 5.1

Community and Population "Niche" Equations

The equations and definitions used are taken or adapted from Lane, Lauff and Levins (1975) and Lane and Levins (manuscript).

Given:

d(ih) = density of population i in habitat h (sampling unit)
E = total number of habitats per environment
N = total number of populations i

1. $$D(i) = \frac{1}{E}\sum_{h=1}^{E} d(ih)$$ average density of population i per habitat h

2. $$D = \sum_{i=1}^{N} D_i$$ average density of community (e) (all populations) per habitat h

3. $$p(ih) = \frac{d(ih)}{\sum_{h=1}^{E} d(ih)}$$ proportion of population i occurring in habitat h of total of population i occurring in all habitats E

4. $$P(h) = \frac{\sum_{i=1}^{N} d(ih)}{\sum_{i=1}^{N}\sum_{h=1}^{E} d(ih)}$$ proportion of all populations occurring in habitat h of total of all populations occurring in all habitats E

5. $$B(i) = \frac{1}{\sum_{h=1}^{E} P^2(ih)}$$ niche breadth of population i

6. $$\hat{B} = \frac{1}{\sum_{h=1}^{E} P^2(h)}$$ community (e) niche breadth

7. $$B(i)/\hat{B}$$ relative population niche breadth, a measure of how much ecological space population i uses as compared to the community (e) use of all habitats

8. $$\overline{B(i)/\hat{B}} = \frac{\sum_{i=1}^{N} B(i)}{N}$$ average relative population niche breadth over all populations i

9. $$\hat{B}/E$$ relative community (e) niche breadth

10. $$\alpha(ij) = \frac{\sum_{h=1}^{\varepsilon} p(ih)\, p(jh)}{\sum_{h=1}^{\varepsilon} p^2(ih)}$$

ecological overlap - measure of overlap of population j on population i based on the probability of co-occurrence of the two populations - alphas can be arranged in a community (e) matrix

11. $$\bar{\alpha}(ij) = \frac{1}{N(N-1)} \cdot \sum_{i \neq j}^{N} \alpha(ij)$$

average overlap value for community (e) matrix

12. $$K(i) = D(i) + \sum_{\substack{j=1 \\ j \neq i}}^{N} \alpha(ij) \cdot D(j) = \sum_{j=1}^{N} \alpha(ij)\, D(j)$$

average carrying capacity of population i per habitat h - carrying capacity is the theoretical density a population would obtain if there were no co-occurers

13. $$D(i) / K(i)$$

co-occurrence success ratio for population i - it measures how well population i has reached its carrying capacity

14. $$\frac{\bar{D}(i)}{\bar{K}(i)} = \frac{\sum_{i=1}^{N} D(i)/K(i)}{N}$$

average success ratio for all populations

15. $$\%\left(\frac{K(i)}{B(i)/\bar{B}}\right) = \frac{K(i)}{\left(\frac{B(i)/\bar{B}}{D}\right)}$$

a utilization efficiency ratio (based on average density for comparison purposes) - measures how well population i could theoretically fill (Ki) the proportion of ecological space (Bi/B) it possesses; since (Ki) depends on the amount of food in each habitat, the general suitability of each habitat for population i, and the safety from predators for each habitat, this ratio measures the relationship of population i to factors and populations in the ecosystem which are not represented in the matrix of co-occurers

16. $$\%\left(\frac{K(i)}{B(i)/\bar{B}}\right) = \frac{\sum_{i=1}^{N} \frac{K(i)}{B(i)/\bar{B}}}{N} \Big/ D$$

average community (e) ecological efficiency (based on average density for comparison purposes)

17. $$Q(i) = \frac{\sum_{h=1}^{\varepsilon} d(ih)}{\sum_{i=1}^{N} \sum_{h=1}^{\varepsilon} d(ih)}$$

proportion that population i in all habitats is of all populations in all habitats

18. $$H = -\sum_{i=1}^{N} Q(i) \log(2) Q(i)$$

total community (e) diversity

APPENDIX 5.2

Sampling Units and Populations Used in Population and Community "Niche" Study

"Leiorhynchus"-Devonochonetes community type

Sampling unit[1]

Population[2]	4	5	6	9	10	11	12	13	14	15	16	18	19	20	21	22	24	25	26	27	28	29	app./#	%
1 devt	12	17	37	53	84	91	93	126	224	303	316	400	385	371	181	171	137	137	150	170	125	310	22/3893	33.4
2 cam	0	0	0	0	0	0	0	27	0	0	23	76	0	0	44	0	0	12	21	30	17	70	9/320	2.7
3 lei	28	31	229	176	116	138	161	203	252	461	382	560	412	546	397	213	205	180	125	150	280	350	22/5595	48.0
4 amb	6	9	16	3	16	24	0	71	170	141	21	47	0	42	29	39	43	25	18	0	0	155	18/875	7.5
5 mucm	0	2	0	0	0	0	0	0	0	0	16	0	0	0	38	31	27	16	20	0	0	130	8/280	2.4
																								94.0%

Chonetes-Ambocoelia community type

Sampling unit[1]

Population[2]	70	71	72	73	74	75	76	77	78	79	80	81	82	84	85	86	88	89	90	91	92	93	94	95	97	app./#	%
1 orb	6	16	6	15	0	6	3	4	8	9	15	0	1	0	0	5	7	2	0	9	1	6	0	2	0	18/121	2.0
2 tro	7	9	75	14	23	15	50	7	2	5	4	1	0	1	1	0	1	0	0	1	0	3	3	0	0	18/22	3.7
3 cho	325	183	352	113	197	127	129	159	161	193	180	63	14	156	116	233	133	50	20	127	169	105	37	210	135	25/3687	61.5
4 amb	76	119	73	57	16	24	27	100	8	51	54	26	14	7	13	35	69	24	1	20	24	31	16	10	5	25/900	15.0
5 cyr	15	8	18	2	6	3	2	15	0	0	5	4	1	2	3	3	1	3	0	4	3	8	4	4	1	22/115	1.9
6 mucm	1	3	3	2	5	2	0	10	4	9	7	1	0	20	2	6	3	1	0	2	1	1	0	9	10	21/102	1.7
7 tyl	4	3	11	1	2	1	2	4	5	8	2	2	1	5	4	9	5	0	0	5	5	3	7	8	5	23/102	1.7
8 sul	0	0	0	0	0	0	0	2	0	0	0	52	5	1	0	0	0	40	1	6	0	0	13	1	0	9/121	2.0
																											89.5%

1. See Table 1.2 for sampling units and their full populations.

2. See Table 1.3 for populations and substratum-mobility-trophic types used in this chapter.

"Leiorhynchus"-Devonochonetes
1. devt = *Devonochonetes setigerus*
2. cam = *Camarotoechia congregata*
3. lei = *"Leiorhynchus" sp.*
4. amb = *Ambocoelia umbonata*
5. mucm = *Mucrospirifer mucronatus*

Chonetes-Ambocoelia
1. orb = *Orbiculoidea media*
2. tro = *Tropidoleptus*
3. cho = *Chonetes cf. lineatus*
4. amb = *Ambocoelia umbonata*
5. cyr = *Cyrtina*
6. mucm = *Mucrospirifer mucronatus*
7. tyl = *"Tylothyris"*
8. sul = *Sulcoretepora gilberti*

APPENDIX 5.3

Random Number Generator

For each population in each habitat (sampling unit) a random number between 0 and 1000 was generated. These were summed and converted to fractions summing to one. These fractions were then multiplied by the actual sampling unit total. In this manner, random numbers were generated for each of the populations for each sampling unit with the total organism count for each sampling unit set to equal the Field Data value for the comparible sampling unit.

To avoid the potential problem of taking contiguous sets of computer generated random numbers, after a batch of random numbers was generated for a sampling unit, up to 1000 batches were randomly skipped before the next batch of random numbers was generated and kept.

Two tests of the randomness of the generator algorithm were made:

1. Kolmogoroff-Smirnoff Goodness of Fit Test

   One thousand populations per sampling unit were assumed and random numbers between 0 and 1000 were generated for each sampling unit. One hundred separate runs were undertaken and 2 of the 100 runs failed the K-S test of uniform distribution.

2. Runs Test

   The K-S data was subjected to serial runs tests for population values above and below the mean. Six of 100 runs failed a $p < 0.05$ t-test for serial randomness.

The generator algorithm is included for reference.

```
]LIST 10,

10  REM  - GENERATOR -
15 D$ = CHR$ (4)
20 H = 3: REM  -  NUMBER OF HABITA
      TS
30 P = 5: REM  -  NUMBER OF POPULA
      TIONS
40  DIM S(H + 1),R(H + 1,P + 1)
52 S(1) = 46:S(2) = 59:S(3) = 282

90 S = 1000:SS = 1001
100  PRINT "------ ------ --------"
120  FOR K = 1 TO H:T = 0
130  FOR I = 1 TO P
140 R(K,I) =  INT (SS *  RND (1))

150 T = T + R(K,I)
160  NEXT I
170  FOR I = 1 TO P
180 R(K,I) = (R(K,I) / T) * S(K)
190  NEXT I
192  FOR L = 1 TO  INT (1000 *  RND
      (1)): NEXT L
200  NEXT K
300  FOR L = 1 TO H
400 G$ = "H" +  STR$ (L)
402  PRINT G$
410  PRINT D$;"OPEN";G$: PRINT D$
      ;"WRITE";G$: PRINT P
430 K = L
440  FOR I = 1 TO P
450  PRINT R(K,I)
460  NEXT I
470  PRINT D$;"CLOSE";G$
500  NEXT L
550  PRINT
600  FOR L = 1 TO H
602 G$ = "HH" +  STR$ (L)
606  PRINT D$;"APPEND";G$
607  PRINT D$;"WRITE";G$
608 K = L
610  FOR I = 1 TO P
612  PRINT R(K,I)
614  NEXT I
616  PRINT D$;"CLOSE";G$
700  NEXT L
800  REM  - NOW LOAD COMMUNITY AN
      ALYSIS PROGRAM -
900  PRINT D$;"RUN MC PCNM"

]SAVE
```

APPENDIX 6.1

Loop Analysis Method[1]

A digraph of the relationships within a system might be drawn as shown below where, for example, X1 could be a prey species such as grass, X2 a herbivore, and X3 a carnivore. Lines between entities show their relationship to one another, a —→ indicates a positive link as might occur when the herbivore feeds on the grass (X1—→X2). This is assigned a +1 value. A —o indicates a negative link as might occur when the grass is consumed by the herbivore (X2—oX1). This is assigned a -1 value.

In this example, the digraph represents a system in which there are two predator-prey links and a self-damping loop for the carnivore. Loops of whatever length are closed paths from an entity to itself without visiting any other entity more than once.

In evaluating the relative stability of this, or any, system, calculations must be made for each feedback level. Feedback level one (1) is for self-loops only. These may be positive (positive feedback) or self-damping (negative feedback) as seen in (X3—oX3). Level two (2) involves all the possible situations where two entities are joined together, either in a closed loop, such as that seen in (X2←—oX1) seen below, or combinations of two self-loops (not shown). Level three (3), and higher levels, involve loops of three or more entities in either closed or disjunct loops as in [(X3—oX3) + (X1o—→X2)].

Thus, a level corresponds to the number of entities involved, and the number of calculations needed at each level depends on (a) the number of closed loops and (b) the number of disjunct loops which do <u>not</u> share a common entity such as the level three loop of (X3 and X1—X2). At each level calculations must be made for each combination of entities, a process that quickly gets out of hand without an appropriate computer algorithm. The value for each loop is determined by the product of its links. If there are an <u>even</u> number of disjunct loops involved, the result is multiplied by -1. Thus, for level one in the diagram the sum of all of the self-loops must be totaled. Since there is only one self-loop, and this is a negative loop with a value of -1, the total for this level is -1. This is termed the F1 value. Similarly, calculations are made for levels two and three with these results: F2 = -2 and F3 = -1.

The criteria for stability in a community analysed by loop analysis are straightforward:

1. Each level (F1, F2, F3, etc,) must have an overall negative result when all the calculations have been performed and summed.
2. Shorter loops (lower levels) should dominate over longer loops in their contributions to stability. Length of loops correspond to length of time-lags and, for stability, shorter time-lags should predominate over longer ones. For systems that are not too large Levins established that (F1)(F2) + F3 must be positive. In this example where F1 = -1, F2 = -2, and F3 = -1: (F1)(F2) + F3 = +1.

By both of these criteria the digraph is of a stable system.

A full presentation of loop analysis and the mathematical theory which supports it is found in Levins (1975) and Puccia and Levins (1985).

---

1. Adapted from Pilette, R., R. Sigal and J. Blamire (1987), *The potential for community level evaluations based on loop analysis*, **BioSystems**, 21:25-32.

APPENDIX 6.2

Basic Assumptions in the Use of Loop Analysis[1]

a) *There is adequate, however incomplete, representation of a system* (Lane and Levins, 1977). Proper characterizations of the interactions and identification of the important entities are necessary and there is an important interdependence of field and lab investigations with theoretical analyses. Loop analysis will not predict a new variable for a system, but the necessity of finding another variable can be inferred from the results. Successful perturbation analysis, such as found in Lane (1986), is an indicator that the system being evaluated is a meaningful one.

b) *The system is at or near equilibrium.* Stability questions "involve the system's behavior around the steady state" (Wright and Lane, 1984). However, nonequilibrium and instability does not preclude the use of loop analysis (Lane and Levins, 1976). Important subsystems may be in equilibrium, quasi-stable regularities may be identified, and one aspect of a system may be in equilibrium (i.e. trophic structure) while another is not (i.e. individual population abundances). Change [e.g. successional -- thus following a predictable developmental trajectory (Salthe, personal communication)] does not necessarily mean nonequilibrium.

c) *The system can be represented by linear relationships between variables.* When a nonlinearity can change the interaction sign, the nonlinearity is obviously important to identify. A known nonlinear varible can be reformulated (Wright and Lane, 1984) or described (Patten, 1979) as a linear one.

d) *Qualitative results may not coincide with quantitative results.* However qualitative analysis can save time and money when an initial overview is sought, indicating the variables of main importance which can be studied in detail. Evaluation of the range of permissible input values may also be undertaken. Finally, with sufficient information, a full quantitative analysis may be undertaken.

1. Adapted from Blamire, J., R. Pilette and R. Sigal (manuscript).

APPENDIX 6.3

Raw data and percentages used for loop analysis in Chapter 6[1]

	below Sulco. layer			Sulco. layer		above Sulco. layer		
	#	%	% differ.	#	%	% differ.	#	%
crinoids								
Deep Spring	8	16.0	+185.7	11	5.6	-76.8	4	1.3
Geer Road	2	8.0	-63.3	7	4.9	-91.8	1	0.4
Lebanon Cen.	2	0.7	+75.0	3	2.8	-28.6	4	2.0
CHENANGO	12	3.3	+31.3	21	4.8	-75.0	9	1.2
Sulcoretepora								
Deep Spring	5	10.0	+63.9	52	27.7	-100.0	0	0.0
Geer Road	1	4.0	+85.6	40	27.8	-100.0	0	0.0
Lebanon Cen.	1	0.3	+95.8	13	12.0	-100.0	0	0.0
CHENANGO	7	1.9	+92.1	105	23.9	-100.0	0	0.0
other Bryozoans								
Deep Spring	0	0.0	+100.0	2	1.1	-36.4	2	0.7
Geer Road	0	0.0	+100.0	4	2.8	-71.4	2	0.8
Lebanon Cen.	1	0.3	+93.5	5	4.6	-78.3	2	1.0
CHENANGO	1	0.3	+88.0	11	2.5	-68.0	6	0.8
nuculanas								
Deep Spring	0	0.0	+100.0	8	4.3	-53.5	6	2.0
Geer Road	1	4.0	-42.9	4	2.8	+25.0	9	3.5
Lebanon Cen.	18	6.2	-121.4	3	2.8	+46.4	8	4.1
CHENANGO	19	5.2	-33.3	15	3.4	-8.8	23	3.1
Chonetes								
Deep Spring	14	28.0	+16.4	63	33.5	+80.3	180	60.4
Geer Road	20	80.0	-130.5	50	34.7	+41.8	133	52.2
Lebanon Cen.	210	72.2	-110.5	37	34.3	+55.4	105	53.3
CHENANGO	244	66.7	-95.6	150	34.1	+63.3	418	55.7
brachiopods (immobile, not *Chonetes*)								
Deep Spring	2	4.0	-25.0	6	3.2	+43.8	12	4.0
Geer Road	0	0.0	+100.0	5	3.5	-22.9	7	2.7
Lebanon Cen.	16	5.5	+1.8	6	5.6	-8.9	10	5.1
CHENANGO	18	4.9	-25.6	17	3.9	0.0	29	3.9
brachiopods (low attached)								
Deep Spring	20	40.0	-121.0	34	18.1	+48.1	80	26.8
Geer Road	1	4.0	+80.1	29	20.1	+77.6	91	35.7
Lebanon Cen.	28	9.6	+66.6	31	28.7	-8.0	52	26.4
CHENANGO	49	13.4	+37.4	94	21.4	+38.8	223	29.7

1. Only populations and guilds comprising greater than 2.0% of the nine sampling units considered here ('other bryozoans' included for comparison purposes.
2. % difference from % value for middle (Sulco.) layer.

APPENDIX 6.4

Scoring of change from before *Sulcoretepora* layer to *Sulcoretepora* layer and from *Sulcoretepora* layer to after *Sulcoretepora* layer

		RN*		%*		%D*		Score	
		before/after		b.	a.	b.	a.	b.	a.
crinoids	Deep Spr.	(+)	-	-	0	-	-		
	Geer Rd.	(+)	-	0	0	-	-		
	Leb. Cen.	0	0	0	0	+	-		
	CHENANGO	+	-	0	0	+	-	+	-
Sulco.	Deep Spr.	+	-	+	-	+	-		
	Geer Rd.	+	-	+	-	+	-		
	Leb. Cen.	+	-	+	-	+	-		
	CHENANGO	+	-	+	-	+	-	+	-
other bry.	Deep Spr.	0	0	0	0	+	-		
	Geer Rd.	(+)	0	0	0	+	-		
	Leb. Cen.	(+)	(-)	0	0	+	-		
	CHENANGO	+	(-)	0	0	+	-	+	-
nucs.	Deep Spr.	+	0	0	0	+	-		
	Geer Rd.	(+)	(+)	0	0	-	+		
	Leb. Cen.	-	(+)	0	0	-	+		
	CHENANGO	(-)	+	0	0	-	0	-	(+)
Chonetes	Deep Spr.	+	+	(+)	+	(+)	+		
	Geer Rd.	+	+	-	+	-	+		
	Leb. Cen.	-	+	-	+	-	+		
	CHENANGO	-	+	-	+	-	+	-	+
brachs. (imm., not Cho.)	Deep Spr.	(+)	+	0	0	-	+		
	Geer Rd.	(+)	0	0	0	+	(-)		
	Leb. Cen.	-	(+)	0	0	0	0		
	CHENANGO	0	+	0	0	-	0	(-)	(+)
brachs. (low attach.)	Deep Spr.	+	+	-	(+)	-	+		
	Geer Rd.	+	+	+	+	+	+		
	Leb. Cen.	(+)	+	+	0	+	0		
	CHENANGO	+	+	+	+	+	+	+	+

* Change Scoring:

Raw Numbers (RN)	% from s.u. to s.u (%)	% difference from Sulco. layer (%D)
>+5 = +	>+9.9% = +	>+24.9% = +
+3 to +5 = (+)	+5.0% to +9.9% = (+)	+10.0% to +24.9% = (+)
-2 to +2 = 0	-4.9% to +4.9% = 0	-9.9% to +9.9% = 0
-3 to -5 = (-)	-5.0% to -9.9% = (-)	-10.0% to -24.9% = (-)
<-5 = -	<-9.9% = -	<-24.9% = -

APPENDIX 6.5

Parameter change evaluation of a digraph

Parameter change evaluation is most fully discussed in Puccia and Levins (1985). The formula is:

$$\frac{\text{(parameter change sign)(link value sign)(F-comp value sign)}}{\text{(F-n sign)}}$$

parameter change sign - is the perturbation effect defined as positive or negative?

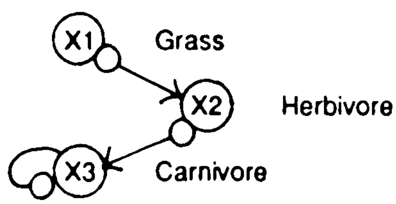
link value sign - what is the value of the link or links from the entity of parameter origin to the entity whose sign value for number change is being evaluated? (A self-path is considered to be positive.)

F-comp value sign - what is the F-value at the (n-k) level for the n-k entities not involved in the link from the entity of parameter origin to the entity whose sign value is being evaluated? (A null system is considered to be negative.)

F-n sign - what is the F value at the n level for the n level system?

A worked example:

Given the system of Appendix 6.1, what would the table of all possible parameter change effects be?



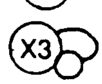
* start by evaluating positive parameter change effects : (+)
* F-n = F3 = (-)

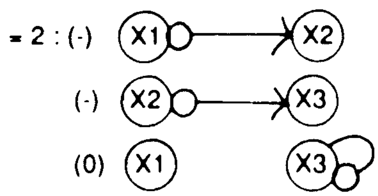
* F-comp for n-k

(n-k) = 0 : (-)

= 1 : (0) 

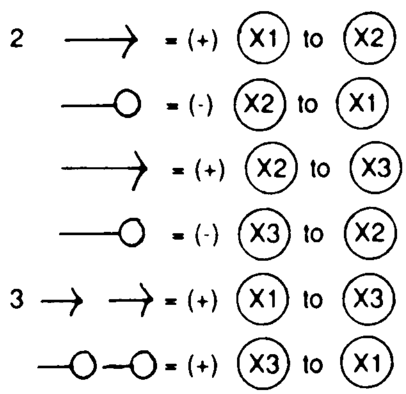
(0) 

(-) 



* link value sign

1 (self) = (+)



RESULTS

		Parameter change effect		
		X1	X2	X3
Origin of positive parameter change	X1	+	+	+
	X2	—	0	0
	X3	+	0	+

Thus, for example, a positive parameter change entering the system through X1 will increase the values of X1 , X2 , and X3 .

The results of a negative parameter effects evaluation will be found by reversing the signs in the table immediatiely above.

APPENDIX 6.6

***Chonetes* measurements (millimeters)**

- measured width along hinge axis
- at least one-half in good condition
- * = measured one-half and doubled result
- measured external preservations only in order to reduce chances of misidentification

Lebanon Center Road			Geer Road			Deep Spring Road		
below	Sulco.	above	below	Sulco.	above	below	Sulco.	above
6.6	6.6	5.9	6.8	3.0	6.5	7.0	3.7	5.7
4.6	4.5	11.5*	3.2	3.6	6.2	5.1*	7.1	5.1
6.5	7.5	4.7	5.8	4.8*	7.5	8.3	4.1	5.4
7.1	5.5	3.9	4.1	5.1	8.2	5.1	8.7	4.7
8.3	5.5	3.7	5.5*	5.3	6.4	5.8	5.1	8.4
6.6*	5.3	10.4	5.0	2.2	6.8	6.2	6.5	6.3
5.4	4.7	3.4	7.1	5.1	8.0*	9.5*	5.8	6.5
4.6	5.1	7.0	8.2*	5.3	6.5	7.4	3.8	7.1
7.1	10.8*	4.6	4.7	4.8	6.4	6.2	7.5*	5.0
5.8	6.3	4.5	6.5*	5.4*	9.2	6.4	6.3*	4.3
4.7	5.6	4.4	4.9	4.1	5.9	10.9*	6.0	4.8
7.5	6.2	2.7	10.7*	5.4	4.8	5.2	6.9	3.2
6.1	5.5	8.7	4.2	4.9	9.5*	8.3	5.0	8.6
6.1	8.0	4.0	7.2*	4.1	7.0	5.6	9.2	9.6
5.4	7.0*	6.6*	5.1	3.8*	6.9	4.5	10.6	4.8
8.0*	4.3	7.1	12.2	5.3*	9.1	5.4	4.1	5.7
4.6	5.7	3.9	4.4	10.1	6.3	4.9	8.2	7.5*
3.6	8.5*	10.0*	3.6	5.9*	4.4	5.2	3.5	6.9*
7.0	5.1	5.5*	7.6	10.7*	6.6	6.3	9.0*	9.6
3.3	6.2	10.9	7.1	5.6	6.4	8.1	2.7	5.3
	4.0	5.6	4.1	4.8	6.9	4.7	6.9	4.6
	7.4	7.4*	2.9	4.1	5.5	4.9	9.3	10.6
	5.5	7.0	2.7	2.6	4.0	3.8	4.4	7.4*
	4.3	4.4	4.9*	5.6	6.4	5.7	3.8	5.7
	6.2	3.5	5.0	4.7	6.3	8.4	5.5	6.8*
	7.4	8.2	5.2	8.6	9.3	4.4	5.5	5.0
	7.0*	6.5*	7.2	9.3	3.7	5.7	10.1	
	8.5		6.6	6.7*	2.9	5.8	9.0	
	5.2		6.1	5.8	5.4	5.0*	4.2	
	10.9*		11.2	6.2	6.1*	4.1	8.2*	
			8.2*	4.8	7.5*	4.5	6.4	
			5.3	8.7*	7.2	5.1	4.3	
			8.8	5.3	6.6	4.8	4.2	
			6.2	4.9	6.3	7.8	8.0	
			5.8*	4.5	7.0	8.5	5.3	
			4.7	7.4*	4.2	4.1	5.7	
			6.0	8.2	7.9*	4.8		
			5.8	11.3*	4.5	6.9		
			4.5	10.8	11.9	7.3		
			5.9	7.7	8.5*	8.0		

Lebanon Center Road			Geer Road			Deep Spring Road		
below	Sulco.	above	below	Sulco.	above	below	Sulco.	above
			4.2	3.9	10.1			
			10.7	11.2	8.1			
			7.1*	7.3*	4.2			
			9.2	12.0*	6.1			
			5.0	12.4	4.4			
			5.6	5.2	7.2			
			7.0	7.4*	5.8			
			3.5	11.4*	3.9			
			5.9	5.8	9.1			
			6.1	8.3	7.7			
			3.7	6.3	5.5			
			5.9	10.9	5.5			
			7.2		6.0			
			6.3		9.3*			
			6.3		6.7			
			12.9		8.2			
			10.2		6.0			
			5.0		4.6			
			4.8		6.2			
			4.6		7.7*			
			5.4		7.6			
			8.9		6.5*			
			4.4		7.7			
			4.3		4.9			
			5.5		4.4			
			5.7		4.2			
			6.7		3.8			
			5.8		3.9			
			6.0		5.1*			
			6.6*		7.0			
			5.9		5.3			
			3.9*		4.9			
			4.4		3.9			
			6.6		7.4*			
			6.3		10.4			
			4.0		9.0			
			7.0		3.9			
			3.6		4.5			
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