THE QUANTITATIVE AND QUALITATIVE SIGNIFICANCE OF FOSSIL AND SUBFOSSIL GASTROPOD REMAINS IN ARCHAEOLOGY

by

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The Quantitative and Qualitative
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Abstract

This study is concerned with the interpretation of gastropod remains from archaeological sites in the Yukon Territory, Illinois and Kentucky. Emphasis is placed on the application of simple statistical models and analyses to the interpretation of prehistoric cultural and environmental shifts. Furthermore, a collation of known modern ecological parameters of the identified species is provided and employed in the qualitative interpretation of paleoenvironmental conditions.

An historical review of molluscan zooarchaeology is presented to show the gradual development of changing research objectives and methodologies in snail analysis. Similarly, a formalized outline of the mechanisms for shell introduction into archaeological sites is presented in detail. These mechanisms are evaluated for their significance in contributing to shell accumulations recovered in both natural and cultural deposits.

Emphasis is also placed on the recovery techniques employed in shell retrieval and the subsequent presentation of numerical data in the published record. Variability in these two aspects is shown to be a significant source of bias in the interpretation of data.

The concept of ecological diversity is examined and a method for its measurement is presented and applied to archaeological gastropod samples. Variations in diversity between samples is shown to be an important element in assemblage interpretations. Similarly, the truncated lognormal distribution is applied to various archaeological samples to illustrate how the representative nature of samples can be statistically assessed. In general, this study illustrates the need for greater rigor in the analysis of gastropod remains from archaeological contexts.

Quotation

Since cultural reconstruction depends on more than the mere inventory of artifacts recovered from a site, molluscan remains, where present, constitute one of the most important components of cultural debris. They preserve well, are readily identifiable, and are susceptible to quantitative analysis. They offer testimony to the source and variety of food supplies, indicate changes in dietary preference or climatic conditions through stratigraphic analysis, ... Since the quantitative investigation of shell middens is a comparatively recent technique, the methods and objectives have varied greatly ... Where analysis has been attempted, there is a wide range in such factors as size of sample, size of screen, number of samples, excavation technique, and statistical method.

Roberta S. Greenwood
(1961:417)

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1. Introduction

In 1975 Karl Butzer (1975:106) wrote an article entitled "The 'Ecological' Approach to Archaeology: are we really trying?", in which he stated:

> Have the 1960's and early 1970's seen the emergence of an effective interdisciplinary approach to the study of man's past? My own personal and preliminary assessment is that this has <u>not</u> happened.

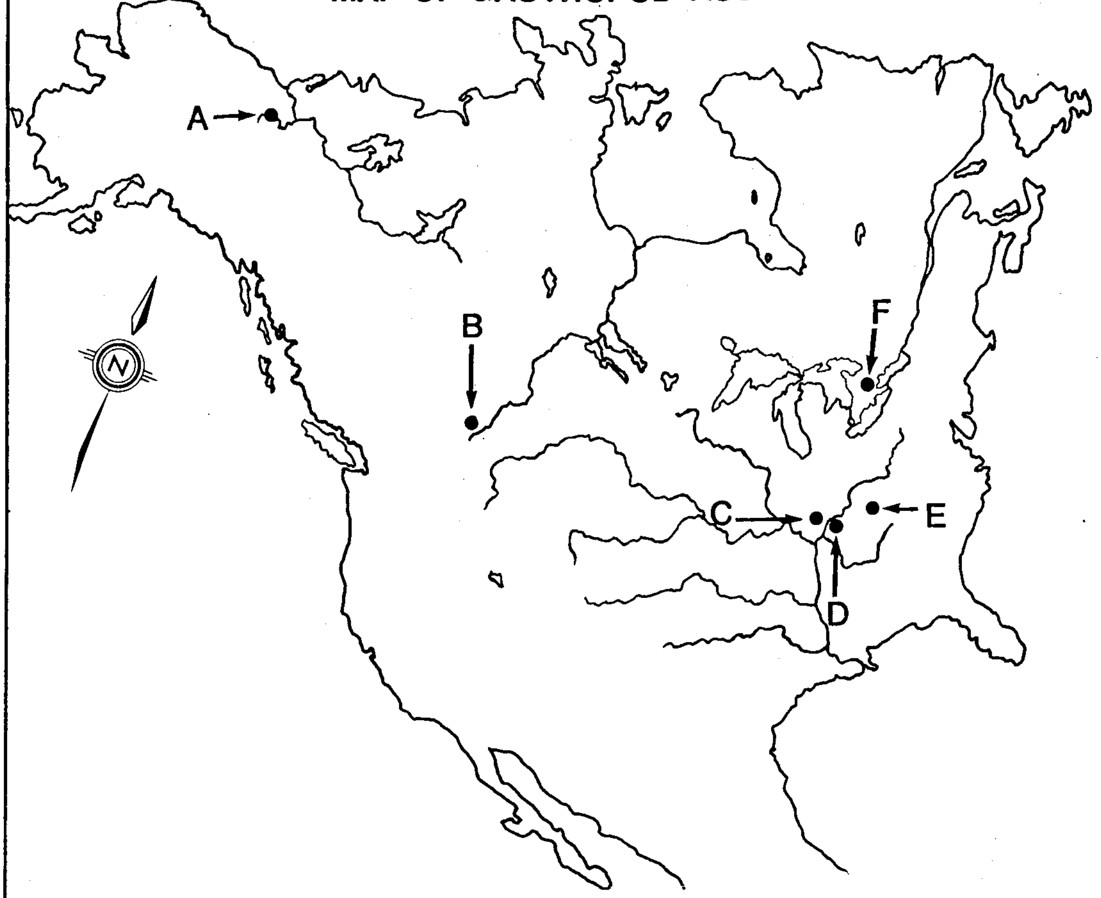
Five years later, Butzer (1980:417) echoed his previous assessment, concluding that "potential contributions from zoo-archaeology, archaeobotany, geo-archaeology, archaeometry, spatial geography, and ecological anthropology continue to be underexploited".

This study responds to the above evaluation by examining and defining the potential information offered to archaeology by the study of gastropod remains. As noted by Greenwood (1961) over twenty years ago, molluscan zooarchaeolcgy is not necessarily a novel subject area within archaeology. However, the goals of research and methodology of analysis continue to be poorly understood and greatly underexploited.

The principal goal of the present research is to provide an interpretation of changing natural and cultural environmental conditions at several archaeological sites (Figure 1). Specifically, gastropod remains recovered from

Figure 1. Map indicating locations of gastropod assemblages examined in this study.

MAP OF GASTROPOD ASSEMBLAGES



A. Old Crow Basin, Yukon Territory

B. Ross Site (DlPd-3), Alberta

C. Black Earth Site (11Sa 87), Illinois

D. Gordon II Site, Kentucky

E. Hall Shelter (15Pe 8), Kentucky

F. Fonger Site (AhHb-8), Ontario

these localities are relied upon as the primary data base for interpretation. In pursuing these objectives, I rely extensively on the theoretical and methodological philosophies of statistics and paleoecology (Ager 1963, 1971; Hecker 1965; Hoffman 1979; Imbrie and Newall 1964; Reyment 1971). By following the approach of quantitative paleoecology, I intend to illustrate through practical examples that gastropod remains from archaeological sites are significant sources of ecological and cultural information to archaeology. The objectives harmonize well with the ultimate reasons for pursuing zooarchaeology within archaeology, that is:

> Biological remains from archaeological sites are examined for three principal reasons: firstly, for their intrinsic interest to biologists and ecologists; secondly, in order to reconstruct human diet and activity; and thirdly, to reconstruct past environments, both local and regional and including human living conditions. (Kenward et al. 1980:3)

Chapter two introduces the subject matter of snails in archaeology with an historical review. This review of past accomplishments is necessary to document the development of current methodolcgical and theoretical reasoning in gastropod analysis. The review culminates with current thought on gastropods in cultural and natural deposits. Under the heading of taphonomy, I examine in detail the mechanisms and reasons for the introduction of shells into sites, and review the effects of cultural and natural agents on gastropod shells. Finally, I justify my basic assumption that the shells examined in this study represent unbiased natural and accidental occurrences.

Chapter three discusses some of the major theoretical and methodological arguments of quantitative paleoecology. First, I review the presentation of numerical data, pointing out the inadequacies and inconsistencies which accompany the reporting of such information. Second, I illustrate the numerical biases which may appear following a poor recovery technique and indicate how gastropod sampling adequacy can be statistically assessed. Finally, I introduce a statistical technique for estimating what percentage of a population's species content is represented in a sample. In brief, this chapter reflects the philosophy I advocate in the quantitative analysis of gastropod specimens from archaeological deposits. In discussing the theory behind this analysis, I perform the basic analyses to prove the theory valid.

Chapter four explores the concept of diversity as it applies to quantitative paleoecology. First, I review the conceptual approaches employed in the examination of diversity. Next, I survey the patterns of gastropod distribution and itemize the limiting factors which account for species diversity. Finally, I examine the measurement of diversity, outline a new method for its measurement, and prove its acceptability by applying it to my own samples.

Chapter five presents the results of analysis of several gastropod samples from archaeological deposits. Each deposit is considered unique and is therefore examined independently of the rest. Within this chapter I apply the reasonings of quantitative paleoecology formulated in chapters two, three and four. Furthermore, I integrate this approach with the qualitative methcdology of paleoenvironmental analysis. The successful integration of quantitative and qualitative approaches will expand the potential contributions of gastropod analysis to archaeology. Chapter six summarizes the objectives and results of this study of snail remains in archaeology.

2. History and Science of Gastropods in Archaeology

This study is concerned with various members of the class Gastropoda within the phylum Mollusca. Molluscs are soft-bodied, non-segmented invertebrate animals that have a foot, head, and visceral hump; the latter typically covered by a mantle which secretes a calcareous shell (Laverack and Dando 1979). In the Gastropoda, the external shell is either saucer-shaped or spirally wound, it covers the lung and intestinal sac, and is usually large enough for the animal to withdraw into for protection or aestivation (La Rocque 1968). The three subclasses of gastropods are the Pulmonata, Prosobranchia and Opisthobranchia. The remainder of this study is not concerned with the systematics or taxonomy of nonmarine gastropods, but rather with their paleoecological significance as it relates to archaeology.

A brief perusal of current archaeological research indicates that gastropods can occur in a variety of deposits, from early hominid sites of South Africa (Brain 1981) to early man sites in North America (Adovasio et al. 1978). A more detailed examination of the North American literature indicates that the occasional reviews of molluscs in archaeology are either: 1) regional in their content (e.g. Alfred 1937; Boekelman 1935; Parmalee 1968); 2) restrictively problem specific (e.g. Jaehnig 1971); 3) very brief discussions (e.g.

Habgood 1968; Lambert 1960); or 4) simply out of date (e.g. Boekelman 1937; Eisley 1937; Wintemberg 1919). A similar state of affairs exists for the literature from the Old World (e.g. Biggs 1969; Butzer 1971; Cameron 1978a; Dimbleby and Evans 1974; Evans 1966, 1968, 1969a, 1969b, 1972; Geyer 1922; Harris 1961; Kennard 1923; Kennard and Woodward 1922; Kerney 1966, 1977a, 1977b; Lozek 1952; Magaritz and Heller 1980; Powell 1959; Reed 1962; Stratton 1970a; Thomas 1978; Turk 1966).

To date, an adequate review of the history of research on gastropods in archaeology has yet to appear in the literature. Similarly, a concise examination of current thought on the subject of gastropods in archaeology has never been attempted. As an historical discipline, archaeology should possess a working knowledge of the chronological developments which have taken place in certain subdisciplines. The history of research on gastropods in archaeology presented in the following discussion fulfills this basic requirement. By necessity, such an historical review ultimately leads to the present, at which point an examination of current scientific thought should be outlined. Under the topical heading of taphonomy, I attempt to answer the basic question, why do snails occur in archaeological deposits? At this point, I emphasize that the discussion on various cultural factors affecting nonmarine gastropods is only significant as part of a comprehensive review. Given the small size of the species examined in this study, their potential use as a food or artifact source is precluded. It should become apparent however, that the past and present accomplishments of molluscan zooarchaeology provide a basis for understanding the future goals and directions of research in molluscan zooarchaeology.

History of the Study of Gastropods in Archaeology

Archaeological attention to nonmarine gastropods dates back to the mid-17th century. Still, one archaeologist concluded in 1972 that:

> the first to notice and comment upon the presence of snail shells in an archaeological context was General Pitt-Rivers (Lane-Fox, 1869,1876) when in 1869 he remarked on the abundance of Cyclostoma (Pomatias) elegans and other species in the ditch of a hill-fort at Cissbury in Sussex, suggesting their use as indicators of the past environment there (Evans 1972:6).

In fact, some 200 years earlier while visiting the site of Silbury Hill in England, King Charles II observed "some of these small Snailes...no bigger than Pinnes-heads, on the Turfe of the Hill" (Charles II quoted in Hawkins 1965:82). Several examples from North America also predate Pitt-Rivers' casual observation. For instance, Brinton (1859:180) notes, "vast aggregations of Helices" in several freshwater shell mounds in Florida as early as 1859. This observation was repeated seven years later in Brinton's (1866) paper on behavioral archaeology. A year later, Wyman (1867) provided what may be the first comment on snail taphonomy, noting that minute snails in archaeological sites are incidental introductions.

Similarly, Evans' (1972) accredition of the paleoenvironmental potentials of gastropods to Pitt-Rivers is also in error. The earliest archaeological attempt at environmental reconstruction using gastropods occurred in North America. Morse (1867:301-302) for example, assessed a treeless shell heap on Goose Island in 1867, by observing "land shells, such as Helix Savii, unidentata, multidentata, and others, remains of which were found in the lower portions of the shell heaps, can only exist in hard wood growths".

One year later, Wyman (1868a:566) not only provided the first complete presence/absence listing of recovered shells in his analysis of fauna from the Crouch's Cove site in Maine, but also added "(t)he presence of so many species of land snails would seem to indicate that the island was once covered with hardwood trees, among which these animals alone flourish". Later in that year, Wyman (1868b) again suggested that the introduction of land snails into Florida shell heaps was purely accidental. Wyman (1875) was also the first to note that the molluscan composition of inland and coastal shell heaps differ considerably, thereby providing the scientific community with one of the earliest attempts at inter-site faunal interpretations.

By 1884 detailed faunal studies from Canadian archaeological sites were entering the published forum. In his discussion of the zooarchaeology of the Bocabec site, Charlotte County, New Brunswick, Matthew (1884:24-25) states "posthumous or accidental additions to the fauna are the land snails, of which several specimens were found at various levels in the shell heaps".

By the late 19th and early 20th centuries, nonmarine gastropod observations from archaeological sites were becoming rote. Eaton's (1898) discussion on the Fort Island, Mott and Cemetery shell middens on Block Island, New England, does not exceed the simple mention of Helix (Anguispira) alternata shells occurring at these sites. Similarly, Loomis and Young's (1912) report on shell middens in Maine, gives only passing reference to Helix shells at several sites. At this time, gastropod remains in archaeological deposits were seen as a source to solving zoological, rather than simply archaeological problems (Johnson 1914). The accomplishments of the first 50 years of research are in fact quite diverse. Beyond simple discovery of gastropod presence, snails were seen as a source of elementary paleoecological information, solutions for certain biogeographical problems, and peculiarities in most archaeological sites whose presence necessitated further attention.

The next decade of study involved greater detail in faunal reporting and continued interest in both taphonomy and paleoecology. Baker's (1923) analysis of bivalves from the Cahokia mounds in Illinois, contains a detailed species list of the recovered gastropods, as well as an observation that their presence was related to introduction by either natural or cultural (i.e. ornamentation purposes) mechanisms. Morse (1925) on the other hand, continued to emphasize the paleoenvironmental potentials of land snails, and thus ignored the critical question of shell introductions into sites (taphonomy).

It was not until 1930, that researchers finally addressed the possibility of gastropods as a prehistoric food resource. At the time, Baker's (1930) reexamination of molluscs from the Cahokia mounds prompted him to include the freshwater genera _Campeloma_, _Anculosa_, _Lymnaea_, and _Planorbis_ as a dietary source in the prehistoric economy. Baker's culinary interpretation of gastropods must have met with some attention, since Ritchie (1932:85) soon added land snails to the prehistoric dietary list at the Lamoka Lake site, New York, noting:

> Twenty-two inches deep on the north side in one of the several small hearths which were found, eighty-four shells of a land snail (_Helix albalabra_) lay heaped as if they had been dumped from a vessel probably after having been boiled for the extraction of the meat.

Baker again pioneered a novelty in zooarchaeology when, in 1932, he attempted a partial quantification of gastropod remains. He described the abundance of one freshwater snail from the Etowah site in Georgia with the statement "more than two score specimens being present" (Baker 1932:148). As discussed in Chapter three, this and later attempts at quantification failed to attract a following in the professional community until the late sixties.

Although casual observations of snails in archaeological sites continued (e.g. Black 1933), some researchers expanded the potentials of snails to include relative dating and paleoclimatology. Schultz and Eisley's (1935) report on the Scottsbluff Bison Quarry, Nebraska, contends that the presence of certain gastropod taxa indicates a very early age for the deposit, as well as a major climatic shift. Indeed, Schultz found great utility in gastropods and managed to assign great antiquity to several other "Early Man" sites in Nebraska solely on the basis of assumed horizon marker gastropod taxa (Barbour and Schultz 1936).

The food resource hypothesis continued to gain favor and color during the 1930's. For example, Huskey's (1935:106) review of archaeological sites in Texas, prompted him to reason:

> Great quantities of snail shells, some burned and blackened by fire, are found at all levels. This leads to the conclusion that the snail was one of the principal food supplies and that a good number were eaten raw.

One year later, it was again Baker (1930) who championed a resourceful approach to data description in the discipline by providing a complete frequency distribution with his systematic list of gastropods from a midden in Peoria, Illinois.

Schultz's relative dating and paleoclimatology applications also attracted a number of followers. Haury (1937) for instance, inferred paleohydrologic patterns at the Hohokam canals, Snaketown, Arizona, on the presence of several aquatic gastropods. Campbell and Campbell (1937) on the other hand, sought refuge in aquatic gastropod specimens to date several sites in Lake Mohave, California.

In the year following Haury's and Campbell and Campbell's work, research on gastropods from archaeological sites assumed greater sophistication. At Blackwater Draw and Anderson Basin, New Mexico, for instance, test pits were specifically excavated with the intention of recovering gastropod shells (Clarke 1938). Although great emphasis was placed on quantitative data for paleoecological interpretations, the reporting of such data was largely overlooked (Clarke 1938).

The importance of gastropods in archaeology during the late thirties and early forties cannot be overemphasized, since the absence of snail shells in cultural deposits was viewed with astonishment by many archaeologists (e.g. Schoenbeck 1939). Snails and archaeology remained firmly joined during the first 75 years of research. Archaeological sites continued to provide zoologists with a source for discovering new taxa (Baker 1942a), while at the same time gastropods furnished archaeologists with clues to paleoenvironmental conditions (Baker 1942b; Roberts 1942). Furthermore, several currently popular topics such as chronostratigraphic applications and food resource potentials of gastropods can attest to their particular usefulness to these formative years.

The year 1942 witnessed the most comphrehensive report yet to appear on snails in archaeology. Archaeological studies in the Pickwick Landing Basin of Alabama by Webb and DeJarnette resulted in an exceptionally detailed analysis of nonmarine gastropods by Morrison (1942). Careful recovery using controlled samples and multiple mesh fine sieving by Morrison (1942), as well as intensive reporting of the data, set a precedent for its time. Gastropods were seen as a source of paleoenvironmental and cultural information, and great reliance was placed by Morrison (1942) on both qualitative and quantitative data.

Unfortunately, the exemplary studies of Morrison and his predecessor Baker continued to be ignored. Cursory mention of gastropods in archaeological sites prevailed through the forties (e.g. Gebhard 1949; Webb and DeJarnette 1948a, 1948b, 1948c) and early fifties (e.g. Aveleyra et al. 1953, Drake 1951; Mayer-Oakes 1955).

In 1953, one proponent of quantitative analyses wrongly criticized Baker's earlier research (see Baker 1936), concluding that Baker's "lists are mainly qualitative in that they are an inventory of the forms present, without the enumeration of individuals represented by the various species" (Matteson 1953a:131). Furthermore, Matteson (1953a, 1953b) seriously challenged the opinion that gastropods found in archaeological sites once served as a food resource. Ironically, Matteson's (1953a) own work failed to enumerate raw data or clarify our knowledge of gastropod taphonomy. However, Matteson did provide the discipline with the belated challenge that gastropods did not contribute to all prehistoric food economies.

The debate on whether or not certain nonmarine gastropods served as a food source continues to the present day. In the late fifties, Matteson (1958, 1959a, 1959b) remained the chief supporter of the natural intrusion hypothesis for explaining snail shell presence in archaeological deposits. Others, such as Fowler and Parmalee (1959) and Parmalee (1958) argued that most snails in sites were culturally introduced as either a food or ornamentation source. A more realistic assessment of this dilemma was finally offered by Hubricht (1954:90), who viewed land and freshwater gastropods separately, leading him to conclude that "aquatic species, as indicated by their abundance, must have been collected locally for food. The land snails were probably attracted by the lime and lived on the mounds".

Most researchers failed to see the relevance in these disputes, simply accepted the presence of gastropods in sites as being of natural origin, and then continued to derive: 1) paleoecological interpretations (Allen and Cheatum 1961; Crook and Harris 1958; Drake 1959, 1960; Meighan 1959); 2) relative age estimates (Allen and Cheatum 1961; Malde 1960; Roscoe 1963; Wendorf and Krieger 1959); or 3) casual publication citations from mollusc remains (Clarke 1963, Drake 1961, 1962; Forrester 1964; Gerow and Force 1968; Parmalee 1960, 1968, 1969).

Hubricht's (1954) sound freshwater/terrestrial dichotomy for examining gastropod introductions into sites became more complex in later years. There were of course the "inclusionists" who viewed both freshwater and terrestrial gastropods as dietary items (e.g. van der Schalie and Parmalee 1960). Others, among the "splitters", remained convinced that only one of the two (aquatic or terrestrial) snails supplemented prehistoric dietary menus (e.g. Webster 1970). Alexander (1963:513) for example, in his analysis of the Levi site freshwater gastropod fauna notes "shells, frequently charred, represent no small part of the inhabitants' diet". Stansbery (1965) on the other hand, viewed aquatic species as purely accidental introductions (an opinion generally shared by others such as Heizer and Napton 1969; Willey and Ruskin 1968) and reintroduced the accessory opinion that some of the land species may have served as a prehistoric food item. The study of gastropods in archaeological contexts developed into a circular argument. Data presentation remained basically abstract, thus precluding any possibility for critical quantitative evaluation of other researchers' work.

Additionally, interpretations were debatable with little or no empirical foundation; aquatic snails were accidental introductions; aquatic snails were prehistoric food sources; land snails were natural site inhabitants; land snails were prehistoric food sources. Scientific advance in molluscan zooarchaeology had reached a snail's pace. Ha Ha Ha

Following Morrison's (1942) exceptionally complete analysis, no outstanding reports on gastropods appeared in the archaeological literature until 1969. Besides outlining recovery procedures and an ecological synthesis, Baerreis (1969) also listed his species frequency distributions. Whereas certain researchers continued to provide only casual mention of snails in sites (e.g. Draper 1969; Janzen 1971; Johnson 1971; Skinner 1971), or elaborate paleoecological interpretations without primary data (e.g. Chace 1969; Hester 1971; Wendorf 1970) in their published reports, Baerreis' (1969, 1971, 1974) efforts did initiate a new trend for detailed reporting (e.g. Brose 1972; Charles 1973; Clench 1974; Gould 1971b; Murphy 1971; Riggle 1976; Wilson and La Rocque 1973).

The last several years of research on gastropods occurring in archaeological contexts superficially appears to be adequate (e.g. Robison 1978). Many studies implement fine recovery methods and attempt paleoecological interpretations on the recovered shell fauna (e.g. Evans 1978; Henry 1978). However, very poor recovery techniques (e.g. Murphy 1973; Tompkins and Dimaria 1979), reliance on small sample sizes (e.g. Evans 1978), and partial data presentation (e.g. Henry 1978) still appear in the literature. All of the above mentioned accomplishments can, however, be integrated under a taphonomic framework in an attempt to understand the reasons for gastropod shell presence in archaeological sites. These historical efforts are credited with structuring the current scientific ideologies of molluscan zooarchaeology.

Taphonomy

Zooarchaeologists and paleontologists have devoted a great deal of effort towards studying the taphonomy of vertebrates. Unfortunately, no systematic taphonomic treatment has yet been attempted for certain invertebrate animals. To fully appreciate the significance of gastropod specimens in archaeological contexts, an examination of invertebrate taphonomy is in order. Thus, in the following discussion, I attempt to review some of the major taphonomic factors which account for the occurrence of gastropods in archaeological deposits. The primary question in molluscan zooarchaeology is, quite simply, what are the major explanations for gastropod presence in archaeological deposits?

There are four primary reasons why gastropods may occur in archaeological deposits: 1) snails were a source of food; 2) the snails represent natural populations once living on the site; 3) gastropods were accidentally introduced into the assemblage; and 4) gastropod shells served a cultural purpose other than a dietary element (Clark 1973; Stansbery 1965). Each of these explanations are explored in greater detail below. Further, observable changes to shell structure resulting from both cultural and natural agents will be briefly reviewed.

i) Dietary Sources

Numerous examples of "escargotieres" from the Old World confirm the belief that gastropods once served as a primary dietary source in certain parts of the world (Lubell et al. 1975). Lacking such convincing empirical evidence in the New World, North American archaeologists have sought refuge in other arguments. The most popular argument on behalf of the food hypothesis is an appeal to analogy. Given the almost universal evidence, both ethnographic and archaeological, for molluscs as prehistoric food sources, many archaeologists intuitively conclude that gastropods were of some dietary import (e.g. Baker 1930; Biggs 1960; Harris 1961; Parmalee 1969; Stansbery 1965; van der Schalie and Parmalee 1960). In the words of one naturalist, these shell deposits are an "extraordinary manifestation of gastronomic power in the aborigines" (Vanuxem 1940-42:21).

A second avenue for arguing in favor of the food hypothesis assumes that high specimen frequencies in the recovered sample is sufficient evidence to substantiate further dietary claims (Parmalee 1969). For instance, Hubricht (1954:90) concludes that "aquatic species, as indicated by their abundance, must have been collected locally for food". However, as will be shown later (Chapter 3), specimen abundance for entire samples is, in some cases, no more than a sampling phenomenon.

A third approach in the food model assumes that charred or burnt mollusc shells indicate their initial use a food element (e.g. Alexander 1963; Clench 1974; Huskey 1935; Robison 1978; Willey and Ruskin 1968). However, natural or accidental fires on the site may result in extensive burning or charring of shell specimens.

Boiling and steaming of gastropods is still another culinary art assumed to have taken place in the past (Clench 1974; Hester and Hill 1975; Kay 1949; Reed 1962). Recent experimental work by Hester and Hill (1975:38) indicates that if snails "are dropped into boiling water, for a very few minutes, the snail will partially extrude from the shell aperture and can easily be extracted" with a mesquite thorn. Lacking a mesquite thorn, Gould (1971b) and Reed (1962) suggest using flint blades, while Clench (1974) recommends bone and wooden needles. In contrast to these observations, Matteson

(1953b:211) notes that "the body of a snail contracts further into the shell when it is dropped in hot water".

This experimental approach to culinary zooarchaeology culminated with Charles Reed's (1962:16) calculated statement:

> It was with pleasurable anticipation, therefore, with respect to the *Helix salmonica* but with some apprehension with regard to the *Levantina diulfensis* that we took more than 300 of the former and more than 200 of the latter and prepared them for eating in the best French tradition ... we had a festive occasion, with special "snail-picks" being provided, made from some of the microlithic bladelets from Tepe Sarab.

Since certain archaeologists remain skeptical of the suggestion that gastropods served as a prehistoric food source in North America (Matteson 1959a, 1959b), proponents of the food model must provide several convincing indications to support such interpretations.

ii) Natural Gastropod Populations

The second major explanation for gastropods occurring in archaeological deposits is that they represent natural death assemblages of the once living communities (Biggs 1960; Matteson 1953a, 1953b, 1958; Stansbery 1965; Willey and Ruskin 1968). This is of course the most reasonable explanation which must be taken for granted unless convincing evidence to the contrary is provided. This explanation forms the basis from which paleoecological interpretations are proffered (Evans 1972). Most taxa found in archaeological deposits reflect the local environment (La Rocque 1966), with the few intrusive forms representing response of neighboring taxa to certain cultural activities such as fire and agriculture (Hubricht 1954; Matteson 1953a; Evans 1972; Tuthill and Johnson 1969).

Before one attempts to understand the taphonomy of snails, that is, the period between death of an animal and its eventual discovery by faunal analysts, a brief comment on gastropod dispersal is unavoidable. This knowledge will explain how snails manage to occur in most sediments on the earth's surface excluding those afflicted by cultural transformations.

Typical gastropod locomotion is accomplished by means of a muscular foot along which peristatic waves of contraction facilitate movement (Laverack and Dando 1979). This form of dispersal is called passive, and can result in colonization rates into ponds in the order of one new species every nine years (Aho 1966; Rees 1965). A second form of dispersal is called chance dispersal. In the latter form, gastropods are introduced into new areas and habitats fortuitously through a variety of agents.

As early as the mid-19th century, Darwin and others suggested both terrestrial and freshwater gastropod taxa disperse by attaching themselves to newts, other amphibians, birds, water beetles, mammals, and floating timbers (Heilprin 1887; Wallace 1876). Following these early suggestions, researchers have documented successful transport: 1) in floating ice and mud (Yen 1947); 2) by attachment to the plumage of birds (Malone 1965; Rees 1965; Sparks 1964a; Vagvolgyi 1975; Yen 1947); and 3) on the legs of many species of insects (Rees 1965; Vagvolgyi 1975).

The strongest arguments favoring chance dispersal emphasize a wind-borne mechanism (Rees 1965; Vagvolgyi 1975, 1978; Wallace 1876; Yen 1947). Although some researchers remain skeptical about this mode of transport (e.g. Croizat 1978), high altitude drag nets have recovered "flying" planorbid snails at heights in excess of 10,000 feet (Yen 1947). One other common mechanism for chance dispersal rarely suggested, is that of transport via the intestinal tract of birds (Yen 1947; Vagvolgyi 1975). Vagvolgyi (1975) cites one example of finding live Succinea species in the digestive crop of an eight hour dead pigeon. However, recent experimental work by Malone (1965) indicates a bird tract mechanism for dispersal to be highly unlikely.

Colonization rates into newly opened habitats vary considerably depending on distance to source, species involved, and chance (Baker 1958). Nonetheless, live full grown snails have been recorded in newly created ponds one day after inundation (Mozley 1928). Thus, natural dispersal can be seen to provide the basis for explaining how gastropods exist in communities on archaeological sites. Unless strong evidence can be presented to show another reason (e.g. cultural) for shell introduction into a deposit, the gastropod assemblage recovered must represent a natural occurrence (i.e. thanatoccenose).

iii) Accidental Shell Introductions

Occasionally, gastropods are accidentally introduced into the natural site assemblage (Wyman 1868b). This third major explanation is difficult to document but is probably a very rare source of bias. Incidental introductions may include shell remains brought onto the site: 1) inside birds and fish (Heizer and Napton 1969); 2) by scavenging animals (Hester 1975); or 3) by other chance means such as attachment to vegetation (Roscce 1967; Willey and Ruskin 1968). For example, Matteson (1959a:54) suggests freshwater snails are "liable to have been carried accidentally with clams" in many cases. Similarly, Morrison (1942:366) insists that aquatic species "must have been introduced in the mud adhering to the mussel shells carried in, or in some cases they were actively adhering to the shells of larger species or to the stones from the river". The precise mechanism of accidental introductions will have to remain largely speculative in the analysis of gastropod samples.

iv) Nondietary Cultural Introductions

The final reason for explaining the introduction of molluscs into the site setting includes all deliberate cultural activities excluding conscious dietary relevance. Parmalee (1958:132) for example, suggests aquatic snails "especially _Anculosa_ sp., were often used as beads". A specimen of the Miocene _Miopleiona indurata_ in the Fogarty Creek site, Oregon, clearly represents a collected curio object (Simon and Reed 1945). Trade items and tool use also explain aberrant occurrences of certain molluscs in many sites (Baker 1930; Boekelman 1937; Curtis 1966; Gould 1971b). Two notable examples of gastropod trade documentation involve the presence of _Cerion incanum_, a Florida Keys land snail, in the archaeological sites of Pecos, New Mexico (Boekelman 1935), and Eiden, Ohio (Murphy 1973).

Finally, it is worth mentioning that snails have been used as feed for both chickens and turkeys (Gould 1971b) and for more subtle purposes by certain Indian groups in Venezuela who recognize aphrodisiac properties in land snails such as _Cerion_ (Gould 1971b), a property which may account for the present day popularity of snails.

v) Gastropod Shell Attrition

Following death of a mollusc, the shell becomes a target for both cultural and natural modifications. With respect to the natural agents, post-mortem preservation and destruction of shells is highly variable. As with pollen grains (Habgood 1968) and seeds (Moore and Wein 1977), gastropod shells vary in their potential durability for preservation (Charles 1973; Parmalee 1956).

According to Evans (1972:19), the proteinaceous shell cover (periostracum) of a gastropod "is destroyed within a year of death, leaving the calcium carbonate exposed to the agencies of physical weathering and solution". Rapid disintegration of gastropod shells thus appears certain in the eyes of some specialists (Evans 1972). Matteson (1953a:131) for example, attempts to explain the absence of aquatic snails at the McGee Creek site in Illinois by stating that "(a)s most of the mussel valves exhibited various stages of disintegration, there is a chance that the relatively frail shells of aquatic snails might have been decomposed". Similarly, van der Schalie and Parmalee (1960) suggest that the low frequency of land snails at the Etowah site, Georgia, is due to the fact that their shells are more fragile and thus not as well preserved as aquatic snail shells. This contradiction illustrates a misunderstanding of shell preservational properties.

According to Raup (1976a) approximately 14.3% of all invertebrate species are gastropods. These 20,000 species represent a major portion of the near 58,000 species of Mollusca currently known (Nicol 1977). Estimates for the preservation of the 58,000 species are in the order of 51,000, which suggests gastropods have a high probability of being preserved. This probability is further confirmed by Lasker's

(1976) recognition that snails represent one of the best preservational classes known among living animals. In other words, nonmarine gastropods preserve very well in many deposits relative to other biological remains.

Freshwater snails appear to have a greater probability of postmortem shell modification than do terrestrial snails. While still in an aquatic medium, freshwater molluscs are subject to heavy mechanical transportation and thus "artificial" accumulations of the shells. In 1901, Wesenberg-Lund (1901) recognized that wave action in lakes occasionally resulted in an artificial shell zone at a depth of 8 to 10 meters below water surface. Since then, this "schalenzone" has been recorded in several other locales (Lepsi 1933; Lundbeck 1929; Pace et al. 1979).

Although models for reworking of aquatic deposits date back to the 1800's (e.g. Heilprin 1887), the degree to which aquatic faunal assemblages are disturbed is not of great concern to most paleoecologists (e.g. Boucot 1953; Fagerstrom 1964; Nave 1969; Peterson 1976; Rigby 1958; Shimek 1913; Zeissler 1971). Several methodological approaches have been employed in the assessment of assemblage disturbance. Absence of land taxa in aquatic samples is one indication of minimal biasing (Mead 1978). Additionally, size frequency distributions, population densities, mortality curves, and other criteria can be used to assess the integrity of death assemblages (Boucct 1953, Boucot et al. 1958; Clark 1968; Craig and Oertell 1966; Craig and Hallam 1963; Hallam 1967; Johnson 1957, 1960; Kranz 1974; Peterson 1976; Rigby 1958; Stanton and Dodd 1976).

Experimental flume studies on orientation of shells have proven to be highly successful with certain invertebrate groups (e.g. Brenchley and Newall 1969; LaBarbera 1977; Nagle 1967; Schwarzacher 1963). Similarly, field experiments on shell movement and orientation in an aquatic medium have provided many useful results with bivalves (e.g. Lever 1958; Lever et al. 1961, 1964; Lever and Thijssen 1968; Menard and Boucot 1951). All of these studies indicate that fossil assemblages occurring in freshwater environments are in fact subject to some sort of reworking, but not necessarily to the point of precluding attempts at paleoecological interpretation.

Post-depositional effects on terrestrial gastropods are less striking than those on aquatic taxa. The major source of post-depositional transport or disturbance of shells in terrestrial sediments is earthworm activity (Cameron 1978a; Dimbleby and Evans 1974). Other factors such as burrowing mammals, trampling and freeze/thaw cycles no doubt play a role in disturbance. Since ecological studies on modern populations of land snails indicate shell orientation is random (Ingram 1944), future experimental studies on disturbance to terrestrial deposits should stress shell orientation pattern recognition.

The final taphonomic factor of concern is that of differential damage to the shell structure and morphology. I recognize three primary agents to shell attrition: 1) cultural; 2) biological; and 3) chemico-physical. With regard to the cultural environment, burning and charring effects on the shell during food preparation have already been discussed. With respect to boiling, Matteson (1959b) notes that nonmarine shells should be either broken or the colored epidermis should flake off the surface. Experimental studies should be attempted before this suggestion is accepted.

Gould (1971b) recognized that over 80% of the Cerion uva shells from three archaeological sites at Curacao, Venezuela, had broken apices. Subsequent experimentation by Gould (1971b) indicated that natural apical attrition was impossible to replicate. Biting the tips of the shells resulted in a "dental misfortune", rubbing was too time consuming, and crushing shells caused the aperture to break first. The only successful method of removing the shell apex was by slicing it off with flint blades. Following this, Gould noted the soft tissue could easily be sucked out through the aperture. A similar hypothesis was offered by Clench (1974), who assumed that the spires of Pleurocera and Goniobasis specimens at Russell Cave, Alabama, were broken off to facilitate apertural removal of the soft tissue. Lastly, artifactual use of gastropods can result in a variety of shell modifications. Morrison (1942:382) for example, recognized that a number of shells "of Anculosa praerosa (a rounded fresh-water snail) were found ground off as if for use as beads or buttons".

Biological persecution of gastropod shells primarily reflects the predatory behavior of certain vertebrates. Atkins' (1966) biological studies in Michigan and Iowa indicate that the spire of Triodopsis is occasionally chewed out by carnivores and rodents. Biggs (1960) cites one interesting observation in which live land snails still attached to bushes had their shell apices eaten by foxes. A variant of this predatory behavior in Texas, involves the crushing of large Rabdotus snails on rocks by "roadrunners". Many nonmarine species are prey to a variety of predators (MacNamara and Harman 1970). For example, Coregonus frequently feeds on V. s. helicoidea (Clarke 1981), while A. alternata is a prey species of the short-tailed shrew (La Rocque 1970). In the end, many biological modifications to shells may mimic cultural actions and should therefore be considered by zooarchaeologists before assuming past cultural actions to be solely responsible.

The final agent promoting shell attrition is that of the chemico-physical environment. Gastropod shell, like bone, preserves best under alkaline conditions (Evans 1972). Disintegration of mussel shells is also very slow in non-acidic soils (Matteson 1960). Sparks et al. (1969:258) suggest the absence of gastropod shells in deposits is due to acid rich sediments or to the fact that shells "are attacked by SO_4 ions liberated by the action of sulphur bacteria" (see also Clench 1926). Acidic soils or mechanical reworking of deposits may therefore result in highly etched or pock-marked shells (Tuthill 1963a). The absence of shell etching has therefore been used as evidence that the samples under question represent stable and relatively undisturbed accumulations (e.g. Leonard 1974). This reliance on negative evidence however, can hardly be condoned.

Summary

In summary, freshwater gastropods are more likely to be subjected to reworking of shells before and after death than are land snails. Terrestrial gastropods on the other hand, usually reflect fairly stable death assemblages. Although a variety of explanations can be offered to account for shell introduction into archaeological deposits, most species examined for paleoecological purposes are too small to be considered representative of deliberate cultural activity. The few taxa which do attain a sufficient size, to either function as a food source or serve an artifactual purpose can usually be examined for changes to their shell surface. None of the larger taxa examined in this study show any sort of post-mortem attrition or modification to their shell surface. Given this observation, all the species recovered and examined in this study are assumed to represent natural death assemblages. Furthermore, the individual assemblages are assumed to be minimally disturbed and contemporaneous with associated cultural materials. Several of the taxa may reflect accidental intrusions into the sample, however, methods for recognizing these taxa have not yet been developed. Moreover, these species simply represent an extension of the habitats represented in a sample and are not considered to be sources of bias.

The history of molluscan studies in archaeology provides an informative indication of disciplinary development. From the earliest observations of snails in archaeological sites to the many imaginative culinary practises, one sees an ever increasing trend in complexity of scientific thought. Gastropods occur in a variety of archaeological settings and attempts at explaining their presence should occupy central concerns in molluscan zooarchaeology. My discussion on the taphonomy of gastropods was intended to reflect the current state of the subdiscipline, to point out a number of extant problems in the interpretation of assemblages, and provide some of the more plausible explanations as to why gastropod shells occur in archaeological contexts. Since the interpretation of gastropod assemblages cannot follow a 'cook-book' approach, one must attempt critical evaluations on a context specific basis. Such a methodology was adopted in the interpretation of individual assemblages examined in this study.

3. Quantitative Molluscan Zooarchaeology

In 1972 J.G. Evans concluded that "until more data can be obtained I feel that statistics will be of little help in assessing the results of snail analysis" (1972:84). This condemnation of quantitative analysis in molluscan zooarchaeology has been termed "quantophobia" (Bobrowsky 1980c). In response to this quantophobia in zooarchaeology, the major aim of this and the following chapter is to indicate the role of quantitative analysis in zooarchaeology.

In a practical sense, an archaeologist begins with a research problem, initiates a sampling strategy, implements a recovery technique, analyzes the recovered remains with certain objectives in mind, and finally, presents the results of the investigation (Binford 1964). In the following discussion I examine the quantitative aspects associated with some of these stages. First, I examine the nature of the published record, since I assume the amount and quality of quantitative data presented in reports generally provide a good indication of the quantitative rigor of the particular study. Second, I critically examine the recovery methodology in shell studies. Within this discussion I illustrate the biases that are involved in various "collection" techniques, as well as comment on the aspect of site sampling. In the latter topic I introduce a new method of quantitatively estimating what percentage of a population is represented by a sample whose initial population is unknown.

Data Presentation

The degree to which a researcher can attempt quantitative syntheses rests solely on the published availability of the required data. Given a basic absence of primary data in the literature, the degree to which quantitative models can be formulated and applied is severely limited. Much of the archaeological, geological and biological literature on molluscs varies in the numerical information contained. For example, many geologists and biologists actively involved in gastropod studies fail to list in their respective reports all of the taxa recognized (e.g. Aho 1966, 1978a, 1978b, 1978c; Benade 1933; Chapman 1919; Cumber 1941; Deevey 1937; Florensov et al. 1978; Gams 1929; Mesyatsev 1924; Mitchell 1948). Fortunately, a great many more of these specialists do at least provide a taxonomic list of species identified in their particular study (e.g. Altena 1957; Blatchley and Ashley 1900; Brown and McDonald 1960; Brown and Bruder 1963; Burch 1955; Call 1900; Chapman 1914; Clayton 1961; Clowers 1966; Cooper 1930; Dexter 1950; Eardley and Gvodetsky 1960; Erni et al. 1943; Frye and Leonard 1963; Gripp and Beyle 1937; Harbort 1910; Hess von Wichdorf 1915; Hollingworth et al. 1950; Hubricht 1961, 1964a, 1964b, 1968, 1971; Jaeckel 1956; Jessen and Milthers 1928; Kennard and Woodward 1922; Kozlovskaya 1951, 1956a, 1956b, 1959; Krausel et al. 1950; Leonard 1974; Lozek 1952, 1962, 1972; McCulloch et al. 1965; Mead 1978; Menzel 1910; Mitchell 1940, 1941; Newton 1910; Price 1900; Roscoe 1963; Roth and Linberg 1981; Tuthill 1967a; Tuthill et al. 1964; Van Damme and Gautier 1972b; Verdcourt 1963; Zoltai and Herrington 1966). Interpretation of such data is limited to simple presence/absence statistical analysis.

The poor practise of omitting numerical data in molluscan studies for both geology and biology is perhaps typical. One malacologist, for instance, states:

> it is worth mentioning that statistical analyses are very time-consuming, and therefore expensive. Furthermore, only very rarely do statistical analyses reveal facts that are not already readily apparent from really competent qualitative collecting. Usually such studies do not produce results that are sufficiently advanced over qualitative work to justify the time and expense involved. (Wurtz 1960:135)

Since archaeologists have relied upon the work of biologists and geologists in malacology, it is not surprising to see archaeological reports with only casual reference to gastropods (e.g Alexander 1963; Black 1933; Boekelman 1935; Drake 1961; Gatus 1981; Gerow and Force 1968; Harrington 1924; Haury 1937; Huskey 1935; Janzen 1971; Murphy 1973; Ritchie 1932; Roberts 1942; Roscoe 1967; Schultz and Eisley 1935; Skinner 1971; Webb and DeJarnette 1948a, 1948b, 1948c; Webster 1970; Wendorf and Krieger 1959; Willey and Ruskin 1968), or detailed taxonomic lists lacking absolute frequency counts (e.g. Anderson 1969; Aveleyra et al. 1953; Baker 1923, 1930, 1931, 1932, 1942a, 1942b; Barbour and Schultz 1936; Biggs 1960; Campbell and Campbell 1937; Chace 1969; Clarke 1938; Clench 1974; Crook and Harris 1958; Curtis 1966; Drake 1951, 1952, 1959; Gardner 1935; Gebhard 1949; Hadlock 1941; Henry 1978; Hester 1971; Hubricht 1954; Malde 1960; Mayer-Oakes 1955; Petit-Marie and Riser 1981; Speck and Dexter 1946; Wendorf 1970).

Occasionally, partial quantification of molluscan remains is presented in a report. This type of data presentation provides relative frequencies or categorical labels to approximate species abundance. Table 1 outlines several relative frequency approaches recognized in the literature. Clearly, the categorical labels between various studies are not comparable. Hence, the application of nonparametric statistics is precluded. These categorical approaches are inappropriate for inter-site comparisons and should therefore be abandoned unless accompanied by both complete frequency distributions and categorical definitions. In this study, the terms abundant (>7% of total), intermediate (3-7% of total), and recedent (<3% of total) will occasionally be used in conjunction with the raw frequency data.

The only totally acceptable form of data presentation is to provide absolute frequency distributions for all of the recovered taxa. Some geologists and biologists do present this

Table 1. Examples of relative frequency and categorical abundance classification schemes.

Aho 1966	dominant = > 7% of total NISP intermediate = 3-7 % of total NISP recedent = < 3 % of total NISP
Altena 1957	! = present !! = more than one specimen !!! = several specimens + = 1-5 specimens ++ = 6-50 specimens +++ = more than 50 specimens
Blatchley and Ashley 1900	Abundant Common Frequent Scarce
Brown and McDonald 1960	A = abundant (10% or more) C = common (2-10%) R = rare (less than 2%)
Clarke 1979a	C = abundant or common R = uncommon or rare
Cooper 1930	a = abundant vc = very common c = common rc = rarely common r = rare vr = very rare
Davis 1954-56	Ab = abundant (over 200 examples) C = common (100 examples)
Dexter 1950	A = abundant C = common N = numerous S = scarce
Grim 1975	A = abundant (21-250 NISP) C = common (11-20 NISP) I = infrequent (1-10 NISP)

Table 1 (continued)

Hollingworth et al. 1950	va = very abundant a = abundant vc = very common c = common r = rare vr = very rare
Jaeckel 1956	sh = very abundant h = abundant s = seldom ss = very seldom
Kaplan and Minckley 1960	abundant = > 50 specimens common = 10-50 specimens rare = < 10 specimens
Kennard and Woodward 1922	v.c. = very common c. = common r.c. = rather common r. = rare v.r. = very rare
Kerney 1971b	a = abundant (> 25 examples) c = common (5-25 examples) r = rare (< 5 examples)
Lozek 1952	abundant sporadic scattered
Lozek 1972	A = abundant x = common - = sparse
Price 1900	very abundant very common common rather common not uncommon not common rare scarce
Rehder 1949	very common common fairly common

Table 1 (continued)

Sparks 1964a	a = abundant (>10% of total) c = common (1-10% of total) r = rare (0.1-1% of total) vr = very rare (< 0.1% of total)
Swadling 1977	1 = 1-9 specimens 2 = 10-19 specimens 3 = 20-49 specimens 4 = 50-99 specimens 5 = 100+ specimens
Webster 1970	common less common
Zoltai and Herrington 1966	abundant = > 5 shells/sq. foot common = 1-5 shells/sq. foot scarce = < 1 shell/sq. foot

basic information (e.g. Ashworth et al. 1972; Farrand and Miller 1968; Getz 1974; Gibson 1967; Hartz and Milthers 1901; Karlin 1961; Kerney 1971a, 1971b, 1976b; La Rocque 1952; La Rocque and Conley 1956; Lundbeck 1929; Miller 1964; Miller et al. 1979; Parmalee and Oesch 1972; Preece 1979; Sparks 1957, 1964b; Sparks and Grove 1964; Van Damme and Gautier 1972a; Zeissler 1971), as well as certain archaeologists (e.g. Baerreis 1969, 1971; Baker 1936; Brose 1972; Charles 1973; Drake 1959, 1960; Evans 1978; Gifford 1916; Heizer and Napton 1969; Matteson 1953b; Murphy 1971; Parmalee 1960, 1967, 1969; Robison 1978; van der Schalie and Parmalee 1960).

The underlying argument of this thesis is basically that all raw (primary) data should be provided for future examination by other researchers. As emphasized and illustrated throughout this thesis, quantitative data have considerable utility in model building, testing, interpretation and critical reevaluations. Measurement of assemblage diversity and the subsequent evaluation of such measures requires clear and concise data presentation. Several examples of quantitative analyses are therefore presented in the discussions on recovery in this chapter, diversity in Chapter 4, as well as in the case study discussions of Chapter 5. The fact that these examples can be presented in this thesis indicates that there is a general trend towards the presentation of raw data in molluscan zooarchaeology, a praise-worthy practise not yet apparent in Canadian vertebrate zooarchaeology (Bobrowsky 1980a, 1980d).

Gastropod Recovery

One commonly ignored concern of paleoecological analysis in zooarchaeology is one's inability to adequately assess inter-assemblage variability (Bobrowsky 1980d). Ultimately, a zooarchaeologist wishes to provide definitive statements on cultural and environmental patterns based on information from several temporally or spatially discrete assemblages. This goal is unattainable if the data from these various assemblages are artifacts of differing recovery strategies. In the following discussion, I examine how variability in sieve sizes hinders adequate gastropod sample interpretation. I also attempt to expose a false belief inherent in controlled weight and volume sampling, and thus argue that sample size should be measured in terms of NISP (number of identifiable specimens).

i) Sieving

Recovery of gastropod specimens from archaeological and paleontological deposits subsumes three numerically interwoven aspects: 1) recovery bias vis-a-vis sieving variability; 2) significance of controlled weight sampling; and 3) significance of controlled volume sampling. Assuming that the latter two aspects are of some importance, it should be evident that inadequate retrieval (no or poor sieving) of gastropods for otherwise controlled samples, invalidates the assumed precision of bulk sampling.

In the following discussion I explore the nature of collection strategies involving casual collection and sieving variations. Although many archaeologists have shown that vertebrate, lithic and botanical materials are subject to various biases when sieves are not used in recovery (e.g. Bobrowsky and Ball 1981), a similar detailing of biases surrounding gastropod recovery is lacking.

Geologists and biologists rely on a variety of techniques for recovering gastropods. These recovery techniques include the use of: 1) cores (Benade 1933; Gripp and Beyle 1937; Harman 1970); 2) augers (Clayton 1961; Leonard 1974; Warner 1968); 3) Hiller type borers (Mitchell 1940, 1941; Norris et al. 1971; Sparks 1962; Sparks and Lambert 1961; Sparks and West 1959); 4) Eckmann dredges (Grimm 1975; Healey 1978; Tuthill and Laird 1963, 1964); 5) drag nets (de Bernardi, Oregioni, and Ravera 1976); and 6) even analysis of common newt stomach contents (MacNamara and Harman 1975).

Archaeologists on the other hand, rely on permutations of two basic techniques to retrieve gastropods from archaeological sites. Incidental or casual collection during excavation is one method of recovering shell specimens (e.g. Biggs 1960; Murphy 1971). The second method of recovery requires some type of screening. The simplest variant of the second technique is use of various mesh sizes on all of the matrix removed from excavation units (e.g. Bailey 1975; Draper 1969; Gatus 1981; Robison 1978; Tompkins and DiMaria 1979; Wendorf and Krieger 1959). Alternatively, sieving of bulk or column samples from excavation units is also a widely used approach (e.g. Baerreis 1971, Evans 1966; Morrison 1942). A third approach to the screening technique involves sophisticated wet sieving and flotation on small subsamples (e.g. Evans 1978; Henry 1978). Finally, various combinations of all of the above (e.g. Anderson 1969; Baerreis 1969, 1974; Mead 1978; Jaehnig 1971) including stacked multiple mesh sieves have also been introduced into the recovery methodology (e.g. Bobrowsky and Ball 1981; Cook and Treganza 1947; Gifford 1916; Voigt 1975).

The earliest documented attempt at sieving sediments for recovering fossil remains is that of Charles Moore, some 100 years ago in England; he apparently sieved some three tons of clay to increase his recovery rate (McKeena 1962; Savage 1960). As early as 1891 in North America, J.L. Wortman transported bagged sediments on horseback for later water sieving (Osborn and Wortman 1892). In 1916, Gifford began using stacked fine sieves to test recovery rates of bivalve remains from archaeological sites in California. By 1936 C.W. Hibbard (1949) had begun using a tub-separation technique (see Bobrowsky and Ball 1981 for terminology) to increase recovery of paleontological gastropod specimens. One year later, J. Morrison (1942) implemented a water sieving technique to retrieve snail shells at several archaeological sites in Alabama. Lastly, in 1953 Vagvolgyi introduced chemical flotation into molluscan retrieval techniques.

All of these major recovery innovations remained forgotten until 1961 when Sparks (1961) demonstrated quantitatively that visual (=casual or incidental) collection of gastropods is biased in favor of larger and more visible (i.e. high color contrast) taxa. Since that time, a variety of mesh sizes have been widely used to recover gastropod specimens. Table 2 provides a range of sieve sizes used by geologists. Relying on the smallest mesh in these 13 cases, the mean sieve opening employed by this sample of earth scientists is 0.473 mm (S.D.= 0.311). Archaeologists also use a variety of mesh sizes for molluscan recovery. Table 3 itemizes this variability for 17 cases. Relying on the smallest mesh in these 17 cases, the mean sieve size in use by archaeologists is 1.83 mm (S.D.=1.93).

Given this spread in preferred sieve sizes, an experiment was initiated to monitor gastropod recovery efficiency as a function of sieve size (see Bobrowsky and Ball 1981 on archaeology). A single 25 cm square column, 2.6 meters in depth, was removed from the Ross site (DlPd-3), Alberta (Figure 1). A sampling interval of 10 cm on the column resulted in 26

Table 2. Mesh sizes employed in the recovery of mollusc shells by various geologists.

SOURCE	MESH SIZE (mm)
Benade 1933	1.0
Clark 1961	2.0, 0.84, 0.42, 0.297
Gibson 1967	2.0, 0.84, 0.42, 0.297
Harris and Pip 1973	0.25
Hibbard 1949	1.19
Kerney 1971a	0.50
La Rocque 1966	6.68, 1.98, 0.83, 0.42
Nave 1969	2.0, 0.84, 0.42
Pauken 1969	0.40
Preece 1979	0.50
Shaak 1976	2.0, 0.42, 0.21, 0.15, 0.125
Shallom 1965	2.0, 0.84, 0.60
Wootton 1975	0.149

Table 3. Mesh sizes employed in the recovery of mollusc shells by various archaeologists.

SOURCE	MESH SIZE (mm)
Anderson 1969	6.35, 3.18
Baerreis 1974	2.0, 0.4
Bailey 1975	8.0, 2.0
Cook and Treganza 1947	2.0, 1.0
Draper 1969	0.159
Evans 1966	0.5
Gatus 1981	1.0
Gifford 1916	12.0, 4.0, 2.0
Greenwood 1961	3.18
Henry 1978	1.0
Jaehnig 1971	0.4
Morrison 1942	6.35, 3.18, 1.59
Riggle 1976	0.42
Robison 1978	1.0
Tompkins and DiMaria 1979	6.35
Voigt 1975	2.54, 0.6
Wendorf and Krieger 1959	6.35

individual samples. Each sample was separately processed through dry sieves of 12.7, 6.35, and 3.18 mm in size. The passed fraction was then water screened through sieves of 1.59 and 0.85 mm. Individual sieve fractions for each sample were then sorted, materials identified, counted and weighed. Table 4 provides a systematic list of the gastropod taxa identified in this analysis.

Out of the 26 interval samples, gastropods occurred in 18 samples (Table 5). No shell specimens were retrieved in the 12.7, 6.35, or 3.18 mm sieves. Assuming total recovery in the 0.85 mm sieve, Table 5 provides the total frequency distribution for the various taxa recovered in the 1.59 and 0.85 mm screens. A comparison of recovery efficiency can then be made between the 1.59 fraction and the total sample. Table 6 outlines the frequency distribution for recovered taxa in the 1.59 mm sieve. As evident in the table, the 1.59 mm sieve failed to recover one or more specimens in 13 level samples. In the remaining five samples, four levels show partial recovery between 50 and 91% in the 1.59 mm fraction (Table 6).

Further, of the 11 taxa identified in the samples, only seven occurred in varying proportions in the 1.59 mm sieve. In terms of the number of identifiable specimens (NISP), the 1.59 mm sieve failed to recover 85% of the total 296 specimens (Table 5). Clearly, all of the sieve sizes greater than 0.85 mm employed in this study are inadequate, since gastropods

Table 4. Systematic list of subfossil gastropod taxa identified from the Ross site (DlPd-3), Alberta.

Phylum: Mollusca
Class: Gastropoda
Subclass: Pulmonata
Order: Stylommatophora

Zonitidae	
Euconulus fulvus	(EF)
Hawaiia minuscula	(HM)
Zonitoides arboreus	(ZA)
Zonitoides cf. *nitidus*	(ZN)
Zonitoides sp.	(ZS)
Endodontidae	
Discus cronkhitei	(DC)
Discus sp.	(DS)
Succineidae	
Succinea cf. *grosvenori*	(SG)
Succinea cf. *avara*	(SA)
Succinea sp.	(SS)
Valloniidae	
Vallonia gracilicosta	(VG)

sp. et gen. indet.

Table 5. Frequency distribution of subfossil gastropod taxa identified by excavation level from the Ross site. (Taxa code taken from Table 4)

EXCAVATION						TAXA						
LEVEL	EF	HM	ZA	ZN	ZS	DC	DS	SG	SA	SS	VG	SUM
1											1	1
5											1	1
8										2		2
9						1						1
10		2					3				3	8
11		2										2
12				2	1	2						5
15			1			1				2	1	5
16						1	1					2
17										1		1
18						3						3
19						2						2
20						1				2	7	10
21			1									1
23					1	1		1				3
24			1			34			1	7		43
25			1			18	2	1	16	20	6	64
26	1		1		31	47	3	4	13	42		142
TOTAL NISP	1	4	5	2	33	111	9	6	30	76	19	296

Table 6. Frequency distribution of subfossil gastropod taxa recovered in the 1.59 mm mesh sieve from the Ross site (DlPd-3), Alberta.

TAXA	EXCAVATION LEVEL 18	19	24	25	26	SUM	PERCENT NISP LOST THROUGH SIEVE
Euconulus fulvus						0	100
Hawaiia minuscula						0	100
Zonitoides arboreus			1			1	80
Zonitoides cf. *nitidus*						0	100
Zonitoides sp.						0	100
Discus cronkhitei	3	1	2	4	2	12	89
Discus sp.					3	3	67
Succinea cf. *grosvenori*				1	3	4	33
Succinea cf. *avara*			1	8		9	70
Succinea sp.				3	7	10	87
Vallonia gracilicosta				6		6	68
TOTAL NISP RECOVERED	3	1	4	22	15	45	—
PERCENT NISP LOST THROUGH SIEVE	0	50	91	66	89	85	85

above 1.8 meters below the surface were not recorded at all. As an additional cautionary note, the efficiency of the 0.85 mm sieve in recovering gastropod shells has yet to be tested.

Ironically, the importance of sieving is largely ignored by researchers. Few geologists (e.g. Frye and Leonard 1963) and archaeologists (e.g. Biggs 1960; Murphy 1971) openly admit to not sieving their samples. Still other geologists (e.g. Ashworth et al. 1972; Blatchley and Ashley 1900; Chapman 1914; Clowers 1966; Eardley and Gvosdetsky 1960; Gripp and Beyle 1937; Kerney 1971a; Kozlovskaya 1951, 1956a, 1956b, 1959; Mitchell 1940, 1941; Norris et al. 1971; Sparks and Lambert 1961; Sparks and West 1959; Warner 1968; Zoltai 1969), biologists (e.g. Atkins 1966; Cantrell 1981), and archaeologists (e.g. Baerreis 1971; Charles 1973; Evans and Valentine 1974) ignore the crucial subject matter altogether. A third group of geologists (e.g. Altena 1957; Altena and Kuiper 1945; Chapman 1919; Cooper 1930; Gould 1970a; La Rocque 1952; Leonard 1974; Sparks 1961), biologists (Harman 1970), and archaeologists (e.g. Baerreis 1969; Evans 1978; Hill 1975; Kenward et al. 1980; Heller and Tchernov 1978; Mead 1978) suggest sieves were employed in recovery, but fail to mention the mesh size. The final conscientious group of researchers not only sieve, but provide details on the mesh size employed (see earlier Tables 2 and 3).

The implications of the sieving experiments and literature review indicate conclusively that intensive retrieval techniques (e.g. flotation or fine sieving) must be used in the recovery of gastropod shell remains. Furthermore, current recovery techniques in archaeology are generally inadequate for significant evaluations to be attempted.

ii) Gastropod Sampling

One of the central concerns in paleoecology is the validity of the samples relied upon for subsequent interpretation. A number of archaeologists have argued that controlled weight or volume sampling is necessary to maintain some sort of analytical precision. The exact logic underlying controlled weight sampling has yet to be fully defined, but Shaak (1976) suggests it minimizes biases. Nonetheless, numerous researchers have recommended various "ideal" sampling weights in their quest for snails. Table 7 itemizes several of these preferred weights in use by geologists and archaeologists. Given the various factors which contribute to sediment weight including percent organic and inorganic matter, types of minerals, percent water and intrusives (e.g. artifacts), as well as the marked vertical and horizontal variability in a given site, it is difficult to imagine the need for sampling by controlled weight. This conclusion is generally shared by most specialists excluding those listed in Table 7 (Green 1979).

Table 7. Suggested sampling weights in use by geologists and archaeologists.

SOURCE	WEIGHT (kg)
Ashworth et al. 1972	15
Bailey 1975	12 - 20
Evans 1966	2
Evans and Valentine 1974	0.5
Greenwood 1961	0.5
Kenward et al. 1980	0.5 - 1.0
Kerney 1971a	2
Kerney 1976b	3
Preece 1979	0.5
Shaak 1976	0.5
Sparks 1961	4.4 - 8.8

Several other researchers suggest that controlled volume sampling is necessary to maintain some sort of precision (Table 8). According to Green (1979:44) "the volume of soil examined from each deposit must be uniform, so that direct comparisons can be made between contexts indicating the actual density" of fossil materials. Furthermore, Green (1979:44) notes that one can "establish the volume of soil removed from a deposit in relation to the volume of the whole deposit". With respect to the latter "calculation", volumetric estimations must be suspect in the 3-dimensional space if most archaeologists cannot adequately define site limits in a 2-dimensional space. This in itself renders volumetric sampling basically questionable.

In regard to the comparison of actual density, the need for density comparisons has yet to be illustrated. Density does not bear any resemblance to diversity. For example, Fisher's (1960) illustrations of increasing calanid diversity towards the the equator can be compared to the documented decrease in calanid density towards the equator. Some other apparent interest in density must therefore be assumed. Although not discussed in this study, it should be evident that various cultural behaviors such as food processing areas may be recognized through a spatial analysis of gastropod density. Therefore, bulk or volumetric sampling cannot be totally dismissed by investigators. Since the gastropods examined in

Table 8. Suggested sampling volumes in use by geologists and archaeolcgists.

SOURCE	VOLUME (litres)
Ashworth et al. 1972	1.0
Atkins 1966	1.0 (sq. meter?)
Baerreis 1971	variable
Blatchley and Ashley 1900	0.53
Cantrell 1981	2.0 (sq. meters?)
Clark 1961	4.72
Clowers 1966	2.0
Evans 1978	60.89
Gatus 1981	variable
Gibson 1967	2.0
Gould 1970a	28.32
Harris and Pip 1973	4.95
Jaehnig 1971	1.0 - 2.0
Kozlovskaya 1951	0.5
Kozlovskaya 1959	1.0
La Rocque 1966	0.79
Morrison 1942	36.82
Nave 1969	4.72
Pauken 1969	28.32
Riggle 1976	4.72
Warner 1968	4.72
Zoltai 1969	1.5

this study are assumed to represent natural accumulations, and are viewed for their intrinsic biological interest, a spatial analysis with the intention of determining intra-site cultural behavior is unnecessary. The following arguments therefore appear to disregard volumetric sampling in favor of element sampling to emphasize the importance of the parameter NISP in species estimates.

Density in itself provides little information of biological interest unless the value is describing an actual population parameter. Seasonal density for example may be quantified for nonmarine gastropod populations. Several researchers have documented marked seasonal fluctuations in gastropod density at various stations (e.g. Cantrell 1981; de Bernardi, Oregioni and Ravera 1976; Dussart 1976; Frank 1959; Strandine 1941a). Repetitive sampling during a single year would indicate "a dominant species in one season may be very scarce in another" (de Bernardi, Oregioni and Ravera 1976:307). Fortunately, fossil and subfossil assemblages represent time averaged communities (Peterson 1976). Species diversity and density in these samples consists of averages over many years. Rates of deposition vary temporally and spatially, allowing for various biases to act on the sample (Baerreis 1971; Sparks et al. 1969). Sparse populations in one portion of a site may appear dense in the fossil record given slow deposition, while rapid deposition in another area with dense populations will appear sparse in the fossil record. Recognition of this depositional variability is limited given poor temporal resolution and variable preservation. Variable preservation does in fact bias the fossil record of density significantly. Seed biologists have recently shown that the durability for preservation of seeds decreases with depth in a deposit (Moore and Wein 1977). A similar situation may exist for gastropods (Bobrowsky 1982a), thus rendering density and not diversity estimates useless. This observation conforms well to the earlier statements on preservation, that is, gastropod species preserve extremely well even though large proportions of individuals of those species do not always preserve well. One paleontologist aptly concluded that "(e)qual volumes of sieved material, while convenient, standardize nothing of biological interest" (Gould 1970a:491).

All ecological sampling revolves around obtaining an adequate representation of the number of species present or an adequate representation of the proportional abundances of those species. Since the number of species recovered increase as a function of increasing sample size, some researchers have suggested optimal NISP values at which point proportional abundance variability in TAXA is greatly reduced (see Chapter 4 on diversity). For pollen analysis, Barkley (1934) recommends NISP values between 175 and 200 to be adequate. Dennison and Hay (1967) note a NISP value of 300 may be sufficient for foraminiferal studies. Finally, for gastropods, Evans (1972) suggests 100 NISP for local environmental interpretations, and between 150 and 200 for broader interpretations. Conversely, La Rocque (1966) assumes 1000 NISP to be adequate for gastropod analysis.

The actual sample size required depends on the confidence limits desired in estimating proportional abundances. Thus, for this study, adequate representation of species with proportions in excess of 3% in the population is desirable (i.e. dominant and intermediate fauna). Using the binomial sampling theory, with p set at 3%, adequate sample size needed is n = 98 for the 0.95 confidence level, n = 151 for the 0.99 confidence level, and n = 174 for the 0.995 confidence level (Dennison and Hay 1967). A similar method of calculating the 95 percent confidence limit can be obtained using the nomograms of Maher (1972).

Even if statistical confidence limits can be applied to the proportional representation of certain taxa in a sample, one is still interested in determining the total number of species actually present in the sampling universe. In an attempt to estimate this species value for the various samples under examination in this study, I applied Preston's (1948, 1962) truncated lognormal distribution for species abundance.

In 1948 Preston presented a series of arguments that indicated that the distribution of species is patterned sufficiently so that a single distributional model could be offered to describe all species abundance distributions. This distribution is described by May (1976:152) who notes that for an assemblage of species "the observed distribution of species' relative abundance, S(N), is almost always lognormal; i.e., there is a bell-shaped gaussian distribution in the logarithms of the species' abundances".

The lognormal distribution requires that individual species be grouped into abundance classes that indicate the number of individuals per species. Each class of the number of individuals per species is called an octave (Preston 1948). Octaves follow the general rule that each interval has a boundary of two-to-one beginning with 1, resulting in the intervals 1-2, 2-4, 4-8 and so on until the maximum interval for the sample distribution is attained. The octaves corresponding to the above log to the base 2 intervals are simply 0, 1, 2, etc.

Since most assemblages can be described as lognormally distributed with respect to the species abundances, one should be able to provide a value of the number of species under the normal curve, that is the number of species in a population or "universe". However, since all assemblages are only samples of the universe, a certain proportion of species may not occur in the sample. That proportion of species not represented in the sample is known as the degree of truncation and can be determined using the truncated lognormal distribution.

The applicability of the truncated lognormal distribution to extant censused biological assemblages has been explored and extensively illustrated for both plants and animals by Preston (1948, 1962). Only recently has the distribution been applied to a fossil assemblage (Koch 1978). In this example, Koch (1978) was able to show that although 175 species of Cretaceous molluscs are presently known, another 25 have theoretically yet to be discovered following increased sampling.

The truncated lognormal distribution therefore possesses an unique character of predicting sample adequacy in population sampling, and should prove useful for most paleoecological studies. By applying this distribution to recovered fossil and subfossil samples, one is able to judge the relative completeness of the sample with respect to the representativeness of the fossil population. Before applying the distribution to the samples examined in this study, I will briefly review the statistical algorithms involved in its application.

As explained by Hald (1952a) the one-sided truncated distribution assumes the point of truncation is known, and that this point is taken as origin for the variable. Using the lognormal distribution of Preston (1948), origin is taken as the '0' from the first class octave interval 0-1. The exact computation of parameters of a normal distribution which is truncated at a known point follows that of Hald (1952a) and is outlined in detail in Appendix IV. In that example, S_0 is the number of species in the lognormal distribution, z is an estimate of the standardized point of truncation, s is an estimate of the standard deviation, and -zs is an estimate of the mean of the distribution (= $\bar{t}$). Additionally, $\phi(z)$ provides the degree of truncation excluded from the original population. Given knowledge of S_0 and $\phi(z)$ one can compute the estimated population frequency $\hat{N}$ which is being sampled. For example, given an hypothetical sample with 15 species (truncated lognormal frequency) and a 25% degree of truncation, the estimated number of species in the universe becomes 20.

From the above one can determine the frequency of species per octave at the mode (y_0) using Preston's (1962) equations. Furthermore, knowledge of the standard deviation of the distribution allows one to calculate (a) which is a measure of dispersion required in fitting a curve to the lognormal distribution. Finally, calculation of the lognormal curve is achieved by the following equation:

$$n = (y_0)\,\underline{e}^{-(aR)^2}$$

where n is the number of species in an octave Rth distance from the modal octave and $\underline{e}$ is the base of natural logarithms (Preston 1948).

The truncated lognormal distribution was then applied to the specific samples examined in this study. Table 9 provides the requisite statistical parameters for each sample. As is evident in these tabulations, each sample shows a different degree of truncation. Three of these truncated distributions are illustrated to show how representation of species composition varies between samples. Figure 2 indicates how an estimated 60.8% of the species in Zone II at the Black Earth site have yet to be discovered. However, since the NISP value for this sample is 298, I am confident that all species with at least 3% proportional abundance have been recorded ($p < 0.001$) and that the remaining 22 species are all incidental.

Figure 3 illustrates a 33.8% truncation for the species sample from Zone IIIA at the Black Earth site. Similarly, Figure 4 indicates a 11.3% truncation for the Level 3, Unit Two sample from the Gordon II site. Once again, NISP values for these 2 assemblages are so high that biasing of the intermediate and dominant taxa is insignificant ($p < 0.001$).

One noteworthy lognormal distribution is that of the Fonger site sample (not illustrated). The raw data for this sample is given in Table 10. According to the principal investigator, gastropod shells were casually collected when observed during excavation (Warrick personal communication). Although 14 taxa were recognized in the highly biased sample,

Table 9. Summary statistics for the truncated lognormal distribution for samples from the Black Earth site, Illinois, the Hall Shelter site, Kentucky, the Gordon II site, Kentucky, and the Fonger site, Ontario.

	BLACK EARTH SITE			FONGER SITE
	II	IIIA	IIIB	
OBSERVED NO. SPECIES	20	14	15	14
LOGNORMAL NO. SPECIES	16.5	12.5	13	11.5
z	0.276	-0.447	0.123	1.501
$\underline{s}$	3.673	3.111	3.058	4.707
$\underline{t}$	-1.014	1.391	-0.376	-7.065
$\phi(z)$	0.608	0.338	0.549	0.933
yo	4.56	2.44	3.78	14.58
a	0.192	0.227	0.231	0.150
PREDICTED NO. SPECIES	42	19	29	172

	HALL SHELTER SITE				
	I	II	III	IVA	IVB
OBSERVED NO. SPECIES	10	9	6	10	19
LOGNORMAL NO. SPECIES	8	7.5	5.5	10	16.5
z	0.859	-0.374	-0.641	0.313	-0.608
$\underline{s}$	2.931	2.281	2.651	3.529	2.466
$\underline{t}$	-2.518	0.853	1.699	-1.105	1.499
$\phi(z)$	0.805	0.354	0.261	0.623	0.271
yo	5.58	2.10	1.05	3.05	3.72
a	0.241	0.310	0.267	0.200	0.287
PREDICTED NO. SPECIES	41	12	7	27	23

	GORDON II SITE			
UNIT ONE	1	2	3	4
OBSERVED NO. SPECIES	15	21	21	13
LOGNORMAL NO. SPECIES	14	18	18	11
z	-0.846	0.091	0.025	0.035

Table 9 (continued)

$\underline{s}$	2.723	4.755	5.101	3.926
t	2.304	-0.433	-0.128	-0.137
$\phi(z)$	0.199	0.536	0.510	0.514
yo	2.49	3.27	2.89	2.34
a	0.260	0.149	0.139	0.180
PREDICTED NO. SPECIES	17	39	37	23

	GORDON II SITE			
UNIT TWO	1	2	3	4
OBSERVED NO. SPECIES	13	17	19	12
LOGNORMAL NO. SPECIES	13	16.5	17	8.5
z	-2.199	-1.505	-1.207	-3.200
$\underline{s}$	1.788	2.500	2.396	0.957
$\underline{t}$	3.932	3.762	2.891	3.060
$\phi(z)$	0.014	0.066	0.113	0.001
yo	2.90	2.87	3.16	3.75
a	0.395	0.283	0.295	0.739
PREDICTED NO. SPECIES	13	18	19	9

Figure 2. Preston's (1948) truncated lognormal distribution for the Zone II assemblage from the Black Earth site.

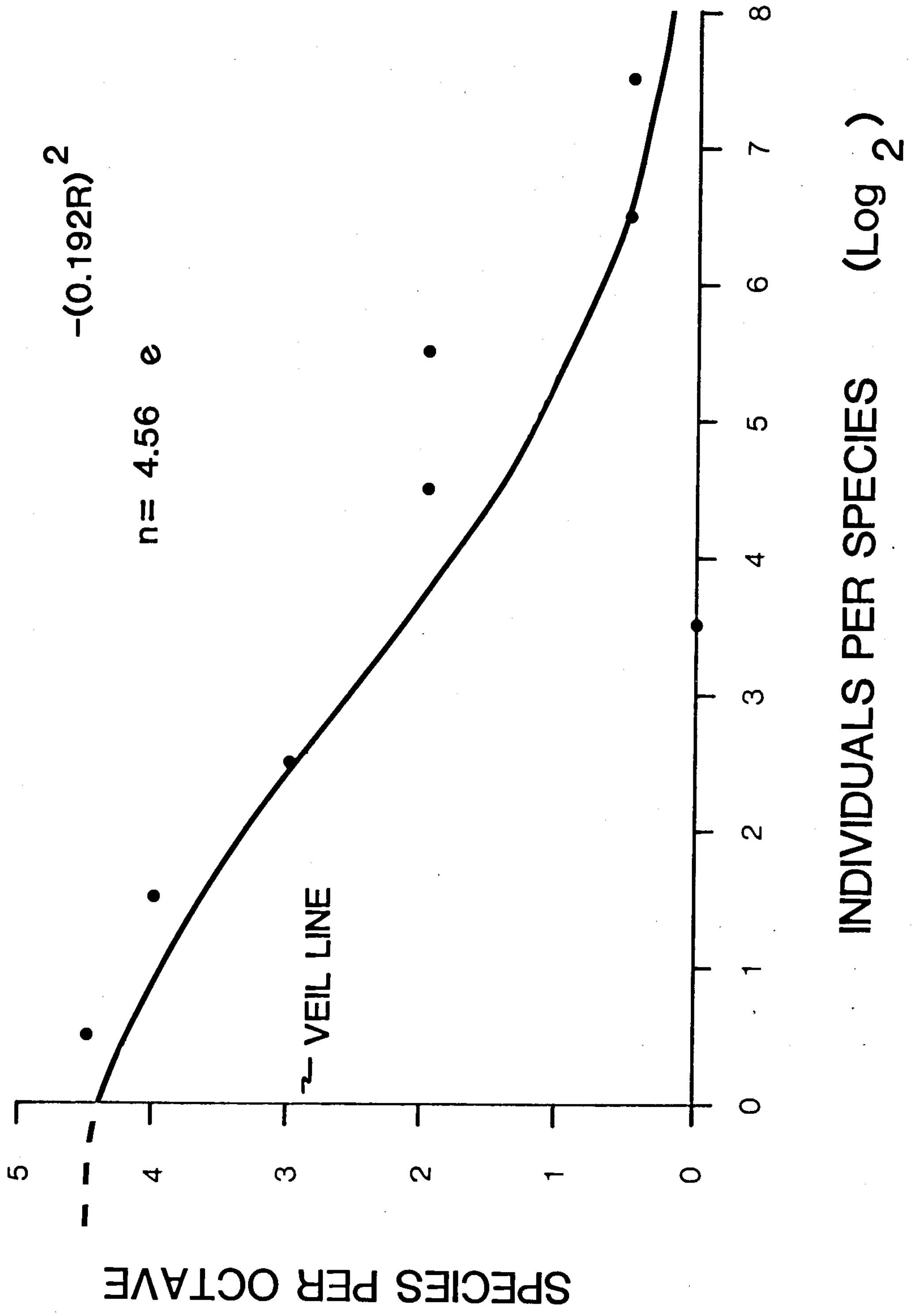

n= 4.56 e^-(0.192R)^2
VEIL LINE
SPECIES PER OCTAVE
INDIVIDUALS PER SPECIES (Log 2)
0
1
2
3
4
5
0
1
2
3
4
5
6
7
8

Figure 3. Preston's (1948) truncated lognormal distribution for the Zone IIIA assemblage from the Black Earth site.

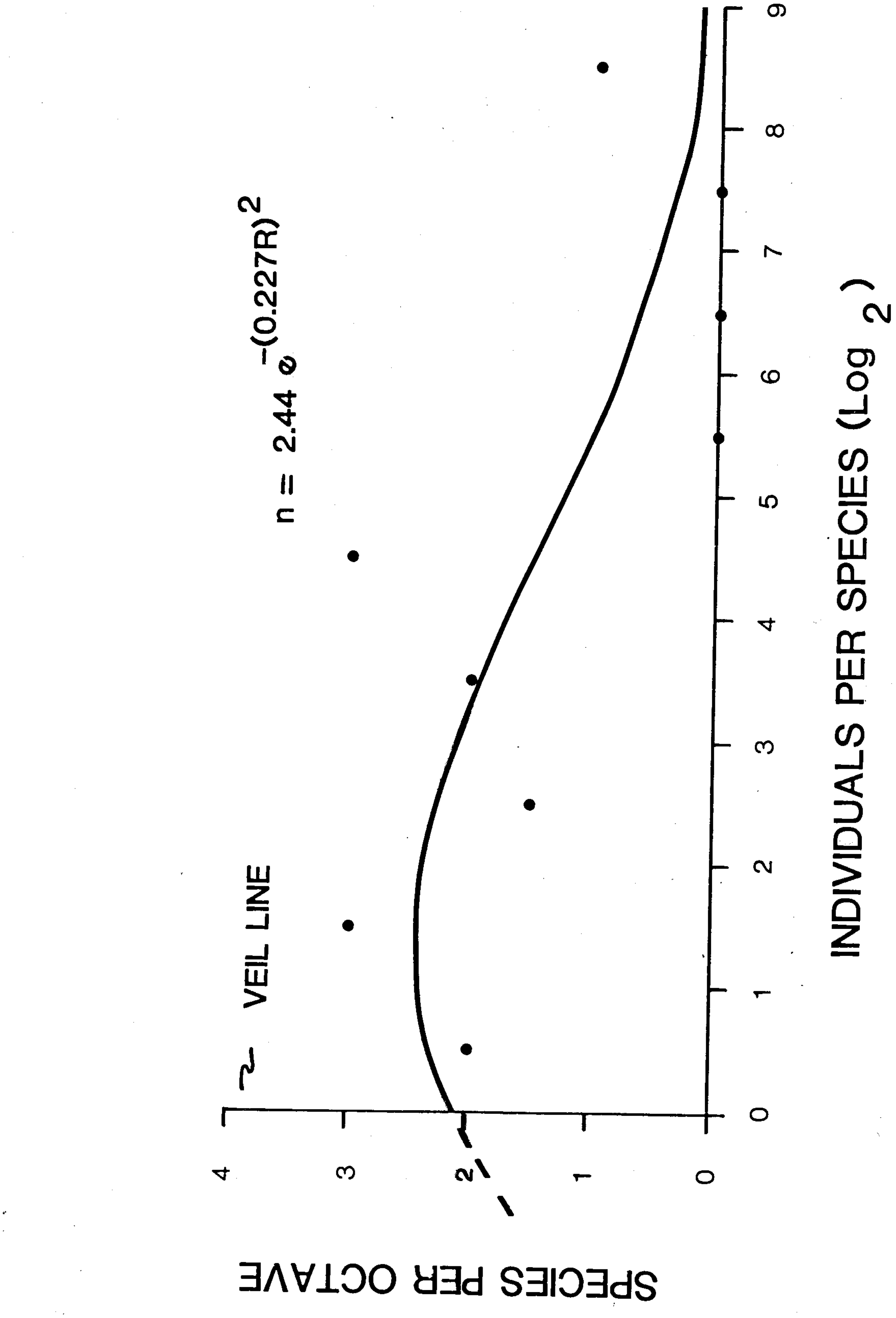

VEIL LINE
$n = 2.44\, e^{-(0.227R)^2}$
SPECIES PER OCTAVE
4
3
2
1
0
INDIVIDUALS PER SPECIES (Log 2)
0
1
2
3
4
5
6
7
8
9

Figure 4. Preston's (1948) truncated lognormal distribution for the Level 3, Unit Two assemblage from the Gordon II site.

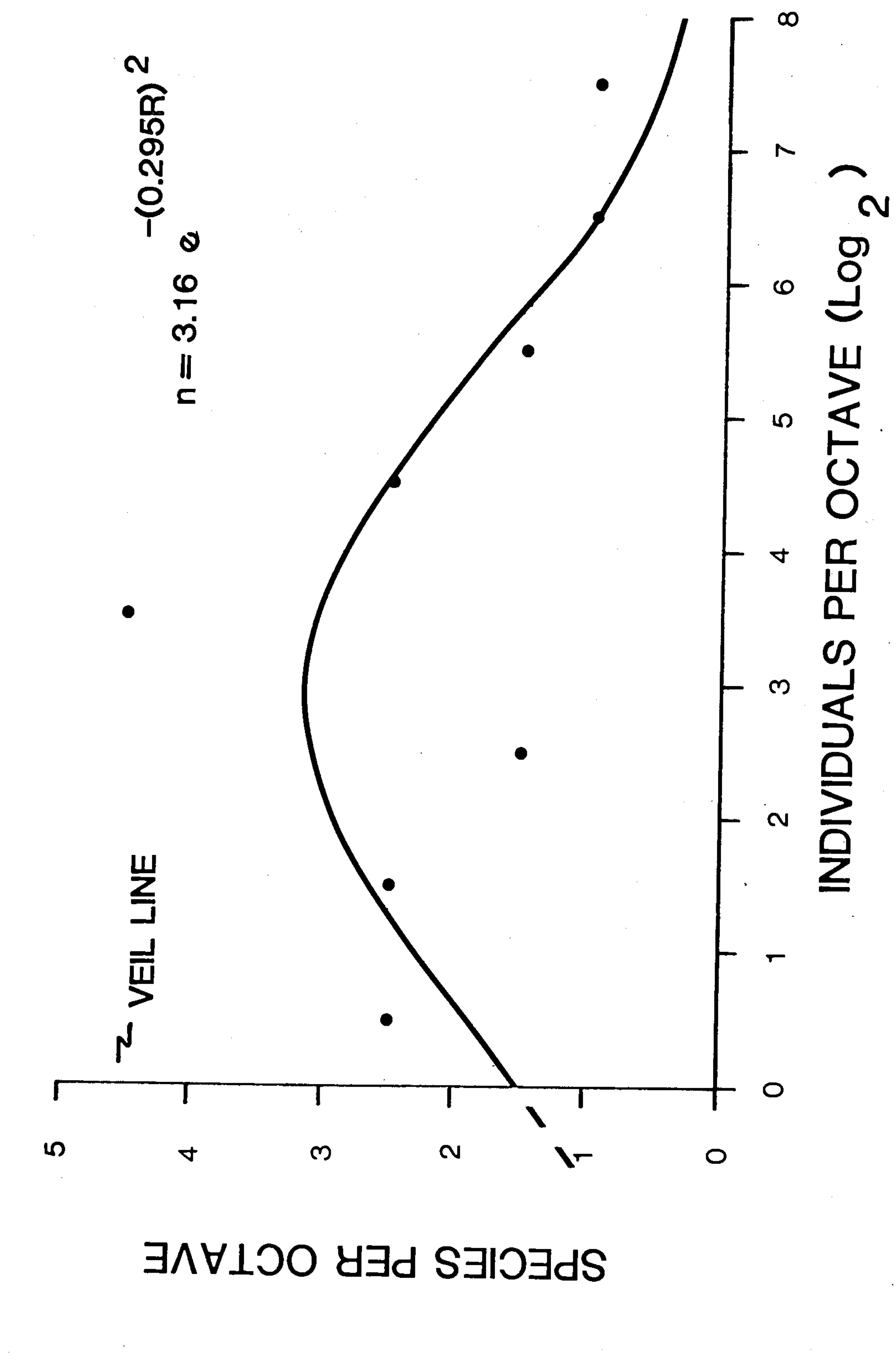

SPECIES PER OCTAVE
0
1
2
3
4
5
VEIL LINE
$n = 3.16\, e^{-(0.295R)^2}$
INDIVIDUALS PER OCTAVE (Log_2)
0
1
2
3
4
5
6
7
8

Table 10. Systematic list and frequency distribution of subfossil gastropod taxa identified from the Fonger site (AhHb-8), Ontario.

	NISP
Subclass: Prosobranchia	
Order: Mesogastropoda	
Family: Pleuroceridae	
Pleurocera acutum	2
Subclass: Pulmonata	
Order: Bassomatophora	
Family: Lymnaeidae	
Stagnicola elodes	1
Stagnicola cf. *elodes*	2
Order: Stylommatophora	
Family: Polygyridae	
Polygyra sp.	13
Mesodon thyroidus	1
Mesodon sp.	2
Triodopsis tridentata	3
Triodopsis denotata	1
Triodopsis albolabris	13
Family: Zonitidae	
Mesomphix cf. *cupreus*	2
Mesomphix sp.	11
Ventridens cf. *intertextus*	1
Ventridens ligera	1
Family: Endodontidae	
Anguispira alternata	89
TOTAL NISP	142

the truncated lognormal distribution suggests that 93.3% of the species in the sampling universe were not recovered. The lognormal curve for this distribution would place the veil line at the extreme right hand tail end of the gaussian curve.

Sampling for gastropod remains in archaeological sites is not a simple operation of controlled weight or volumetric sampling. Each site, with its accompanying strata, varies considerably in its molluscan composition, thereby eliminating any potential for cook-book approaches to sampling. However, if zocarchaeologists establish their research objectives clearly before initiating excavations, pertinent questions may then be addressed within a rigorous quantitative framework (Bobrowsky 1980d). As illustrated above, the adequacy of data on species proportional abundances may be evaluated statistically. Further, the application of statistical distributions such as the truncated lognormal distribution can be shown to be of use in estimating what percentage of species in a universe are not represented in a sample.

Summary

The preceding discussion showed how vital numerical data are tc zooarchaeological analysis. The coverage of statistical zooarchaeology was not extensive but did serve to indicate that there exists a great deal of room for improvement in quantitative studies. In the specific case of retrieving gastropod specimens for paleoecological analysis, one wishes to obtain a sample which will adequately reflect proportional abundances of intermediate and dominant taxa. The lognormal distribution was shown to be a useful mathematical distribution for assessing what percentage of rare species in a population were not recovered in a sample. Similarly, the technique employed in the actual collection plays an important role in providing samples that are unbiased estimators of the particular parameter in question. Poor recovery techniques result in biased material recovery, and thus limit further interpretive potentials. Finally, explicit presentation of primary data (i.e. frequency distributions) is imperative for further assessments and evaluations by other researchers.

4. Diversity in Molluscan Zooarchaeology

It is a phenomenon of the organic world that there are spatial and temporal patterns in the distribution of plant and animal species. A basic understanding of nonmarine gastropod distributions in relation to these two dimensions is, therefore, necessary to fully appreciate the significance of sampling and the subsequent quantitative interpretation of subfossil gastropod assemblages. In the following discussion I address three major questions: 1) what are the patterns of species distributions; 2) what are the limiting factors that control gastropod distributions; and 3) how can variations in species distribution be measured? First, I introduce diversity, an ignored concept in zooarchaeology. Definition of this concept is then followed by illustrations of its application to nonmarine gastropod assemblages. Next, I review the biological and physical factors limiting gastropod distribution and diversity. Finally, I present a new method for measuring diversity of gastropod samples. An examination of these questions and topics will thus provide the basis for understanding the interpretive approach used throughout this study.

Diversity

The distribution of species is best examined by the concept of diversity. However, conceptual approaches towards diversity vary considerably. The oldest and simplest approach views diversity in terms of species richness (McIntosh 1967). First quantified by Fisher et al. (1943), species richness is defined as "the number of species present in a collection containing a specified number of individuals" (Hurlbert 1971: 581). A second aspect to diversity is equitability and evenness, which describe the relationships of abundance in the distribution of species. The dual-concept of diversity, termed heterogeneity by Good (1953), takes into account both richness and evenness (Peet 1974). Mathematical attempts at measuring "diversity" are discussed later in this section.

Spatially, following Whittaker (1965, 1972), diversity can be grouped into an hierarchical scheme. Alpha diversity, represents the lowest level of description, and is a descriptor of intra-community or within habitat diversity. Beta diversity reflects a second order description of diversity changes along an environmental gradient. Finally, gamma diversity is a composite of the above two and thus describes diversity of the entire landscape.

Subsumed under these three levels of diversity, are environmental patches, and the species occupying them. A patch "is a unit of habitat in which the great majority of its interactions with its environment (both biotic and abiotic) take place" (Osman and Whitlatch 1978). Patches can be both continuous and discrete units, which vary in size depending on the taxa under examination (Osman and Whitlatch 1978). Starting with a virgin patch (0 species), species enter the unit at a varying rate of colonization, attain noninteractive equilibrium and eventually interactive equilibrium (Osman and Whitlatch 1978).

This change in diversity with time is termed succession. The earliest taxa to enter the analytical unit are typically called pioneer species (opportunistic), later species which enter into the unit are called stable equilibrium species (climax) (Levinton 1970). Deviations from the deterministic successional model presented above are due primarily to periodic perturbations to the unit. Following Peterson (1977) and others (e.g. Bretsky and Bretsky 1975), perturbations or disturbances are assumed to reduce the number of climax species, promote survival of the opportunistic species, and thus result in low diversity communities.

i) Gastropod Distributions

There are an adequate number of examples to illustrate that the three levels of diversity exist among nonmarine gastropods. Within-habitat diversity has been documented by several authors (e.g. Cameron 1978b; de Bernardi, Oregioni and Ravera 1976; Dussart 1976; Harman 1972; Heilprin 1887; Horst and Costa 1975; Lassen 1975; MacNamara and Harman 1975;

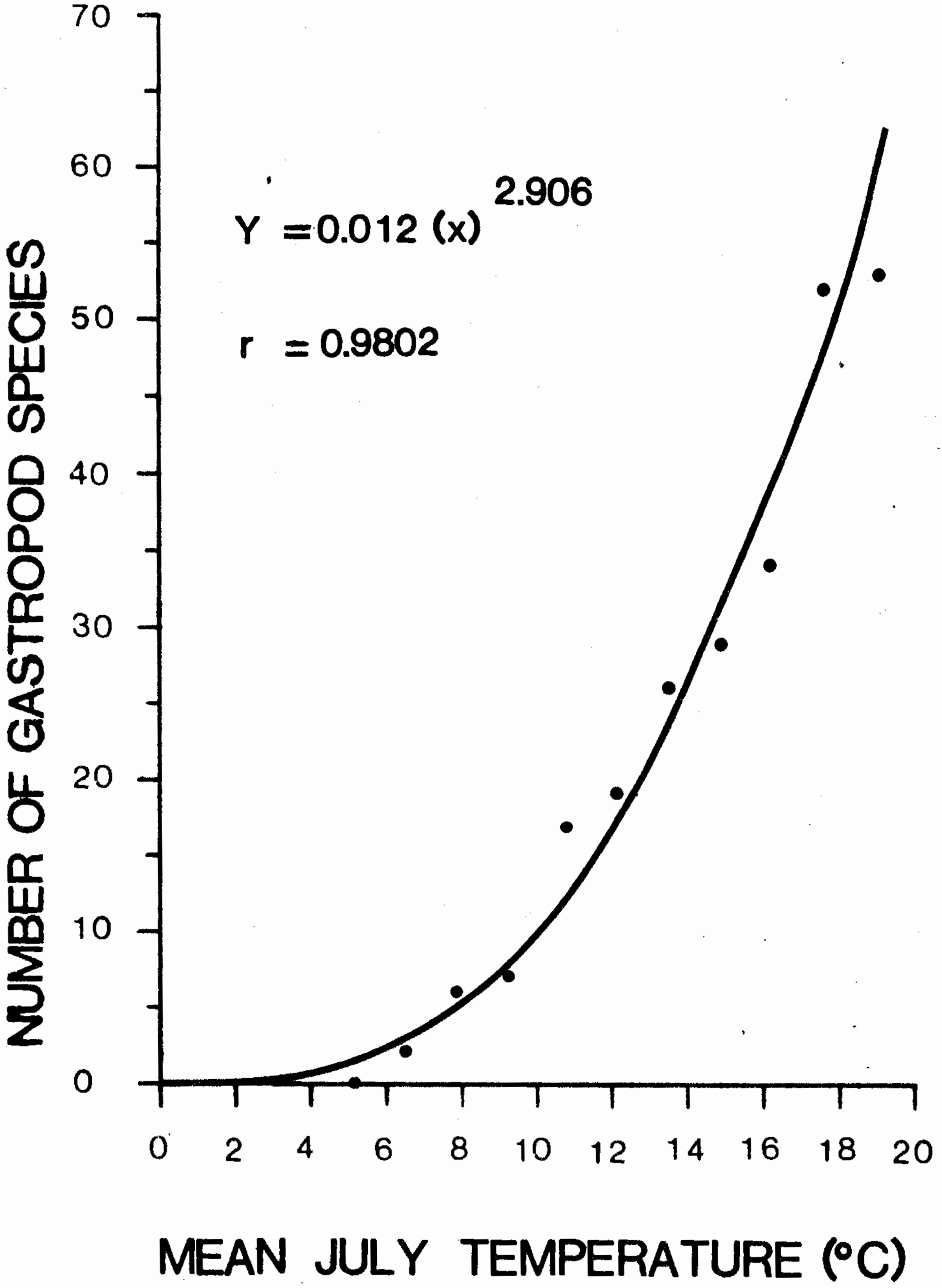
McKillop and Harrison 1972; Riggle 1976; Strandine 1941a). Similarly, beta diversity for gastropods occurs along both aquatic and terrestrial environmental gradients. Harman's (1970) transects through Green Lake, New York, Dexter's (1950) transect through Dollar Lake, Ohio, and Pace et al.'s (1970) samples from Lake Michigan all indicate diversity changes along an aquatic environmental gradient. Getz (1974) and Harris (1978) provide examples of diversity changes along a terrestrial environmental gradient.

In terms of gamma diversity, there are several examples for marine invertebrates (e.g. Raup and Stanley 1971; Stehli 1965; Sanders 1968), large mammals (e.g. Simpson 1964), small mammals (Graham 1976), and plants (Whittaker 1965, 1972) that show a definite pattern in latitudinal diversity exists for many organisms. According to Pianka (1966), latitudinal diversity has not yet been documented for freshwater invertebrates. Following Fisher's (1960:69) observation that "temperature is the main factor in the climatic control of marine plant and animal distributions", as well as the suggestive latitudinal paralleling of temperature gradients in North America, I measured changes in species richness as a function of mean July temperature for freshwater gastropods. Employing the data of Clarke's (1973) extensive survey of freshwater gastropods in Canada, a Model I least squares regression equation was calculated for the data pairs: number of species and mean July temperature. As shown in Figure 5 the relationship is strongly correlated. This indicates that an allometric increase in gamma species diversity is a function of temperature. Hence, gastropod diversity in a latitudinal framework can be shown to exist, as in the case of most other plant and animal species (Fisher 1960; MacArthur 1965; Pianka 1966; Simpson 1964).

Having illustrated that nonmarine gastropods are distributed in varying patterns, one may then address the factors which actually govern gastropod species distribution. Among the aquatic gastropods Aho (1966), Clarke (1973), and McKillop and Harrison (1972) have all shown that diversity is strongly correlated with calcium concentrations in the water. However, diversity can also be shown to be strongly correlated with: 1) humus (Aho 1966, 1978b); 2) pH (Aho 1966); 3) alkalinity (Aho 1966), and; 4) electrolytic conductivity (Aho 1966, 1978b). Similarly, land gastropod diversity can be shown to be correlated with: 1) potassium (Burch 1955); 2) phosphorous (Burch 1955); 3) pH (Burch 1955; Paul 1978; and Riggle 1976); 4) organic matter (Burch 1955); 5) magnesium (Burch 1955; Riggle 1976); and 6) calcium (Burch 1955; Geyer 1922; Gould 1970a, 1971b; Neck 1976; Paul 1978; Wallwork 1970).

Several researchers assume that food availability ultimately controls species distributions and thus suggest that both aquatic and terrestrial molluscs show greatest diversity

Figure 5. Best fit curve illustrating the relationship between the number of freshwater gastropods and the mean July temperature in °C. (Raw data from Clarke 1973).


70
60
50
40
30
20
10
0
NUMBER OF GASTROPOD SPECIES
$Y = 0.012 (x)^{2.906}$
$r = 0.9802$
0
2
4
6
8
10
12
14
16
18
20
MEAN JULY TEMPERATURE (°C)

where food plants are most abundant (Burch 1956, 1957; Danglade 1922; Dexter 1950; Evans 1972; Getz 1974; Karlin 1961; Reed 1962; Shimek 1930a). All of these limiting factors exert some control on species distributions but the "ultimate" controlling factors agreed upon by most researchers are temperature and moisture (Eisley 1937; Evans 1969a, 1972; Getz 1974; Gould 1970a; Habgood 1968; Harman 1970; Harris and Pip 1973; Machin 1967; Miller 1975, 1978; Taylor 1960; Thomas 1978; Tuthill 1963b).

Ecological data on individual taxa in relation to all of these controlling factors varies considerably. This indicates the partial inadequacy of ecological information on most taxa, as well as the bias which accompanies most ecological studies. Data which are collected by researchers on specific species typically reflect the predilections of the researchers involved, since different researchers observe and measure different environmental parameters for the species under study. Hence, a synthesis on ecological requirements of species must of necessity emphasize different environmental parameters. Bearing this limitation in mind, the brief ecological descriptions provided in Appendix V vary in the type, amount and detail of information available on each species identified in this study. Furthermore, as is evident in Appendix V, limiting factor importance varies between species.

ii) Measurement of Diversity

As shown in the preceding sections, the concept of diversity is applicable to nonmarine gastropods as it is to other plants and animals. Similarly, since the distribution of gastropod species can be shown to be controlled by numerous limiting factors, both species diversity and ecology may be used to infer ecological conditions from fossil and subfossil gastropod samples. By measuring species richness and abundance of certain taxa, and by relating these to known ecological requirements, one can propose prevailing dominant environmental conditions for particular communities.

The first step in such an analytical procedure requires knowledge of ecological requirements for the individual taxa in a community. This information has been compiled in Appendix V. The second step in this procedure involves the adequate measure of species diversity. In the following discussion, I review the concept of diversity and discuss the indices used in quantifying the concept. As noted earlier, diversity can be defined in terms of heterogeneity. Thus an heterogeneity index measures both species richness and evenness. Indices in this category include those proposed by Simpson (1949), Shannon and Weaver (1949), McIntosh (1967), Pielou (1975, 1977), Hutcheson (1970), Williams (1964), and Cuba (1981). Besides certain mathematical limitations inherent in these measures, Peet (1974) condemns each on the basis that one is not really sure, for a given index, what parameter is being estimated. Each of these indices mathematically favors either richness or evenness, rendering the two variables interdependent. Any attempt at defining both richness and evenness by a single value (heterogeneity) results in a loss of information and an inability to directly compare two or more differing measures (May 1975, 1976).

As an alternative, the evenness of species distributions has been measured relative to some specific standard, resulting in what is termed an equitability index of the species abundance distribution (Peet 1974). The comparative standard of reference employed in the calculation of equitability is generally a model of a theoretical distribution. Included in these species abundance distributions are the Niche Preemption Model, Broken Stick or Resource Apportioning Model, Overlapping Niche Model, Truncated Negative Binomial Distribution, Logseries Distribution, and Lognormal Distribution (Pielou 1975). As stressed by Peet (1974), equitability measures are inherently dependent on species richness. It is therefore advisable to simply interpret evenness in an assemblage directly by examining the raw frequency distributions. This simple and unbiased methodology is adopted in Chapter 5 for the analysis of several gastropod assemblages.

The problem still exists that alpha, beta and gamma diversity for gastropods is a recognizable phenomenon. Thus some quantitative measure must exist to characterize each of the three levels of diversity. I suggest that species richness provides the most suitable measure for quantifying diversity.

One of the simplest approaches for such a measure is the absolute species count. Given an hypothetical sample, the number of species observed by the researcher provides a measure of species richness (MacArthur 1965; and Williamson 1973). As a partial variant of this method, the average number of species from several samples can be employed (Whittaker 1972; Whittaker and Woodwell 1969; Woodwell 1967). However, the number of species in a sample is a function of sample size (Gleason 1922, 1925; Barkley 1934; Fisher et al. 1943).

In an attempt to circumvent the problem of sample size dependency, several researchers have proposed universal species richness indices (Fisher et al. 1943; Mehinick 1964; Odum et al. 1960; Preston 1948; Whittaker 1972). The validity of these indices, however, requires that two assumptions be satisfied: 1) that the functional relationship between the expected number of species ($\widehat{TAXA}$) and the number of identifiable specimens (NISP) is constant between communities; and 2) that the functional relationship is known (Peet 1974).

Assuming a constant functional relationship, the second assumption is mathematically accessible. The first assumption is basically ignored or assumed in the indices proposed by the various researchers. The relationship between TAXA and NISP is in fact constant, but not between communities. Thus individual functional relationships must be derived for different "communities".

To establish the nature of the relationship between the two variables TAXA and NISP for nonmarine gastropods, I collected information on these data pairs from the published literature. Note was taken as to the general age and geographical location of the sample deposits. Furthermore, data pairs for freshwater and terrestrial samples were kept separate. These divisions of age, space and taxonomy limit information loss of grouped data and can thus be used to examine constancy between communities. Appendix I provides the raw data for all of the data pairs employed in the analyses. Appendix II provides a list of those samples relied upon in the separate spatial, temporal, and biological analyses.

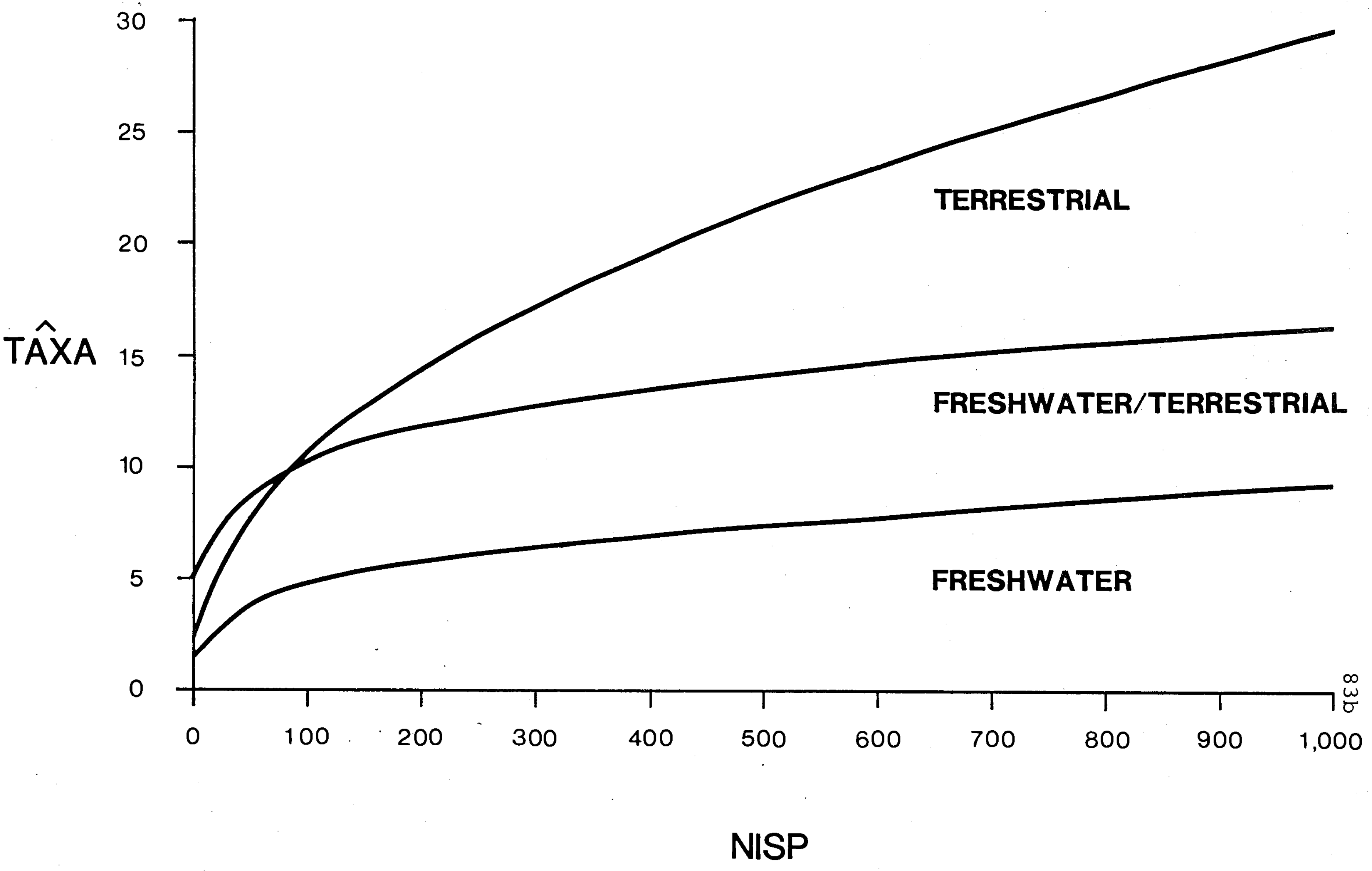
All of the data pairs were compiled into a file on the MTS computer facilities at Simon Fraser University. Model I least squares regression on natural log transformed data was then calculated for various sample groupings (see Kuhry and Marcus 1977). Regression equations describing the relationship between TAXA and NISP were determined spatially for England, North America, and all countries represented in the sample (termed "universal"), temporally for the interglacial, glacial, Holocene, and Quaternary (i.e. all samples less than two million years old), and finally, biologically for freshwater snails (Mesogastropoda and Basommatophora), terrestrial snails (Stylommatophora), and nonmarine gastropods in general (Prosobranchia and Pulmonata).

Table 11 lists the resulting regression equations for the various permutations of $\widehat{\text{TAXA}}$ and NISP mentioned above. The summary statistics for each of these equations is given in Appendix III.

As suggested by MacArthur (1965) there is a theoretical limit to diversity. Given a specific class of animals, there is a maximum number of species that can occur in an area regardless of the number of individuals actually counted. For example, in England there are only 46 species of freshwater gastropods (Kerney 1976c), but 117 indigenous terrestrial species (Walden 1976). Sampling distributions for freshwater and terrestrial gastropods should vary accordingly (see Flessa 1975, for similar taxonomic nesting).

Figure 6 illustrates the functional relationships between $\widehat{\text{TAXA}}$ and NISP for North American Quaternary freshwater, terrestrial, and mixed assemblages; equations 15, 13, and 21, respectively. As in the case of England's gastropod fauna, land and aquatic snails in North America have different diversity limits and should therefore be examined separately. Relying on data from several countries for the Quaternary, a similar pattern is observed to that from only North America (Figure 7).

Figure 6. Best fit curves for North American Quaternary freshwater, terrestrial and general nonmarine gastropod assemblages, illustrating the relationship between the number of species (TÂXA) and the number of identifiable specimens (NISP). (Equations 5, 13, and 21).



TÂXA
30
25
20
15
10
5
0
TERRESTRIAL
FRESHWATER/TERRESTRIAL
FRESHWATER
83b
0
100
200
300
400
500
600
700
800
900
1,000
NISP

Figure 7. Best fit curves for "universal" Quaternary freshwater, terrestrial and general nonmarine gastropod assemblages, illustrating the relationship between the number of species ($\widehat{\text{TAXA}}$) and the number of identifiable specimens (NISP). (Equations 8, 16 and 24).

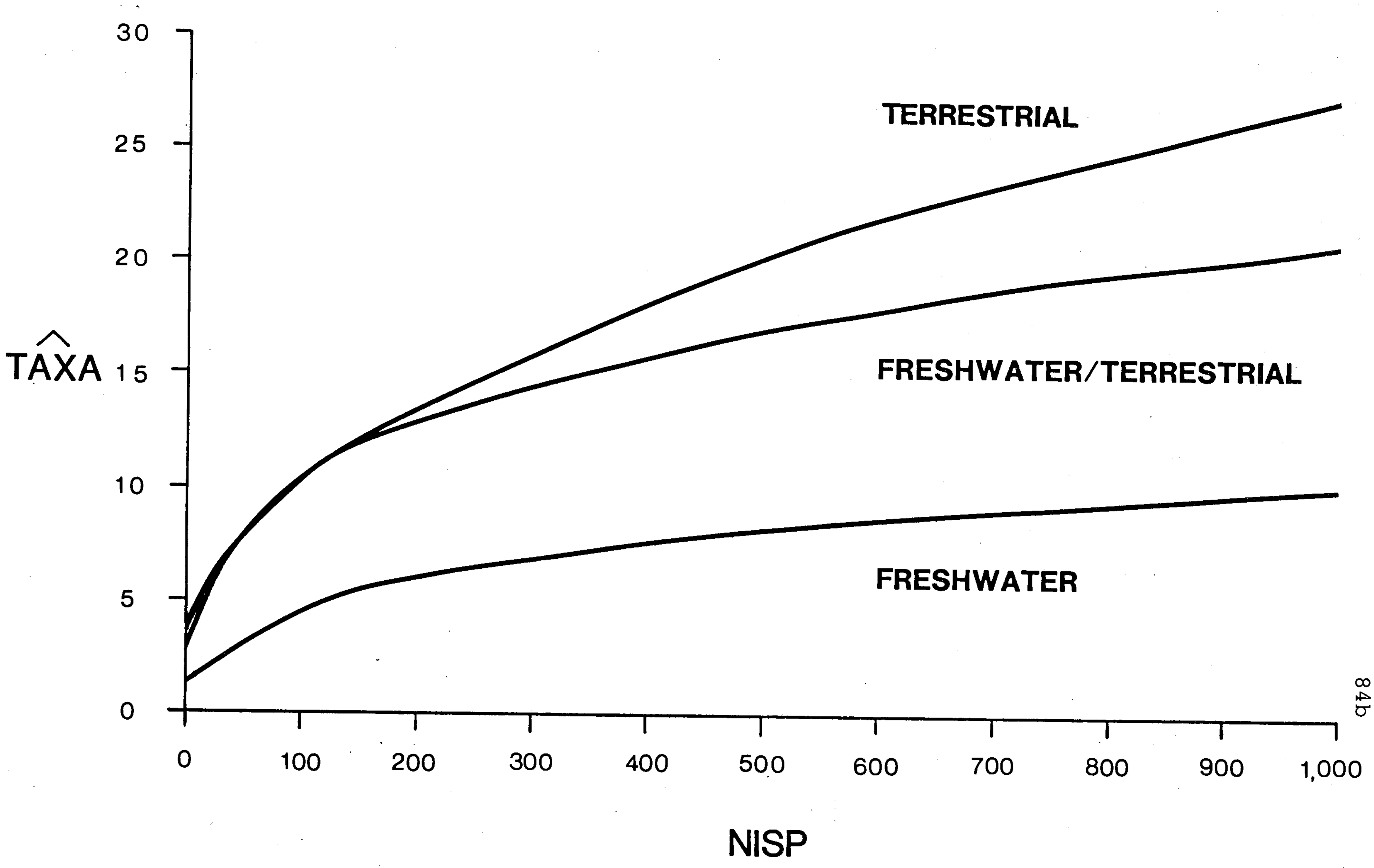

TERRESTRIAL
FRESHWATER/TERRESTRIAL
FRESHWATER
$\widehat{\text{TAXA}}$
30
25
20
15
10
5
0
0
100
200
300
400
500
600
700
800
900
1,000
NISP

Table 11. Regression equations describing the relationship between the number of TAXA and NISP for various faunal, spatial and temporal groups.

FRESHWATER		
ENGLAND		
QUATERNARY	$\hat{T} = 1.032\ (\mathrm{NISP})^{0.349}$	(1)
INTERGLACIAL	$\hat{T} = 1.658\ (\mathrm{NISP})^{0.314}$	(2)
GLACIAL	$\hat{T} = 2.487\ (\mathrm{NISP})^{0.265}$	(3)
HOLOCENE	$\hat{T} = 0.865\ (\mathrm{NISP})^{0.292}$	(4)
NORTH AMERICA		
QUATERNARY	$\hat{T} = 1.206\ (\mathrm{NISP})^{0.296}$	(5)
GLACIAL	$\hat{T} = 1.293\ (\mathrm{NISP})^{0.286}$	(6)
HOLOCENE	$\hat{T} = 8.682\ (\mathrm{NISP})^{0.320}$	(7)
UNIVERSAL		
QUATERNARY	$\hat{T} = 1.128\ (\mathrm{NISP})^{0.318}$	(8)
TERRESTRIAL		
ENGLAND		
QUATERNARY	$\hat{T} = 1.778\ (\mathrm{NISP})^{0.389}$	(9)
INTERGLACIAL	$\hat{T} = 1.280\ (\mathrm{NISP})^{0.541}$	(10)
GLACIAL	$\hat{T} = 1.973\ (\mathrm{NISP})^{0.283}$	(11)

Table 11 (continued)

HOLOCENE $\hat{T} = 2.100\ (\text{NISP})^{0.376}$ (12)

NORTH AMERICA

QUATERNARY $\hat{T} = 1.494\ (\text{NISP})^{0.432}$ (13)

GLACIAL $\hat{T} = 1.403\ (\text{NISP})^{0.437}$ (14)

HOLOCENE $\hat{T} = 1.451\ (\text{NISP})^{0.505}$ (15)

UNIVERSAL

QUATERNARY $\hat{T} = 1.641\ (\text{NISP})^{0.407}$ (16)

MIXED FRESHWATER/TERRESTRIAL

ENGLAND

QUATERNARY $\hat{T} = 2.165\ (\text{NISP})^{0.348}$ (17)

INTERGLACIAL $\hat{T} = 2.143\ (\text{NISP})^{0.359}$ (18)

GLACIAL $\hat{T} = 1.956\ (\text{NISP})^{0.302}$ (19)

HOLOCENE $\hat{T} = 6.904\ (\text{NISP})^{0.384}$ (20)

NORTH AMERICA

QUATERNARY $\hat{T} = 4.282\ (\text{NISP})^{0.194}$ (21)

GLACIAL $\hat{T} = 8.078\ (\text{NISP})^{0.083}$ (22)

HOLOCENE $\hat{T} = 1.741\ (\text{NISP})^{0.421}$ (23)

UNIVERSAL

QUATERNARY $\hat{T} = 2.724\ (\text{NISP})^{0.295}$ (24)

These curves do not reflect a perfect correlation between the variables $\widehat{\text{TAXA}}$ and NISP (Appendix III). Although all of the equations maintain high correlation coefficients, and error in the dependent variable is minimized, several factors must be recognized as contributing to this variability around the best estimate. This variation around the best fit line is expected on practical grounds, since the samples employed reflect: 1) individual researcher experience (taxonomic skill); 2) researcher preferences (taxonomic splitters and lumpers); 3) recovery techniques; 4) preservational biases; and finally, 5) true variation in community diversity (Bobrowsky 1980c, 1982b; Casteel n.d.; Tuthill 1967b). Since the intercept value (a) is a redundant biological parameter, but a necessary statistical parameter in the description of functional relationships, some researchers depend on the slope value (b) to decribe diversity (Pielou 1975, 1977). Unfortunately, as outlined above, four other factors besides diversity contribute to the calculated functional relationships. By controlling for variability in the first three factors, and assuming preservational biases are not species specific, deviations from the best estimates reflect variations in sample diversity. In other words, if the observed value (TAXA or T) is greater than the estimated value ($\widehat{\text{TAXA}}$ or $\hat{T}$) the sample in question is highly diverse. An overestimation in $\widehat{\text{TAXA}}$ relative to the observed TAXA value indicates lower diversity. This diversity can be numerically simplified when TAXA is compared to $\widehat{TAXA}$ in ratio form. Perfect prediction relative to observed values results in the base line ratio of 1.00, so that increasing species richness is evident when the ratio index is greater than 1.00 and lower species richness is evident when the index value is less than 1.00. This methodology is examined in greater detail in the following discussion.

Recalling the strong correlation between species richness and mean July temperature, there should also be a marked difference in species richness between warmer interglacial and Holocene assemblages, and colder glacial assemblages. This theoretical proposition was subjectively established by Sparks (1964:337) in his description of a gastropod sample from Grantchester, in which he states "(t)he interglacial quality of the fauna is evident from the great number of species...Cold deposits may yield great numbers of molluscs, but they usually belong to far fewer species".

To test these assertions of warm-high diversity and cold-low diversity relationships, one can compare the behavior of the regression equations for such a dichotomy. Figure 8 illustrates the variation in species richness for North American terrestrial gastropods in glacial (cold) and Holocene (warm) samples. The theoretical and intuitive arguments (e.g. Evans 1972; Harris 1961, 1968; Heller and Tchernov 1978; and Kerney 1977a) appear to be quantitatively verified here and

Figure 8. Best fit curves for North American glacial, Holocene and general Quaternary terrestrial gastropod samples, illustrating the relationship between the number of species ($\widehat{TAXA}$) and the number of identifiable specimens (NISP). (Equations 13, 14 and 15).

elsewhere (e.g. Burchell 1969; Gould 1970a; Harris and Pip 1973; Lozek 1972; Shaak 1976; Sparks 1964a).

However, the differences in species richness for warm and cold assemblages simply reflects differences in the periodicity and magnitude of environmental perturbations. Since human activity can behave as an environmental perturbation (e.g. agricultural practices), species richness will respond in accordance. The problem which faces individual researchers is one of differentiating between natural (e.g. Bretsky and Bretsky 1975; Gould 1976; Harris and Pip 1973; Jillson 1980; Karlin 1961; Osman and Whitlatch 1978; Peterson 1977; Walker and Alberstadt 1975; Whittaker 1972) and cultural (e.g. Evans 1968, 1972; Evans and Valentine 1974; Kerney 1966; Wallace 1876) environmental perturbations in accounting for observed diversity fluctuations. In this study I assume that the cultural interpretations of archeologists are correct in so far as I rely on their evaluations in differentiating between cultural and natural perturbations.

The actual computation for estimating species richness diversity for individual samples is relatively straight forward. An observed value of NISP for a given sample is replaced for the NISP variable in a chosen equation which best fits the sample in question (i.e. North America, Quaternary, terrestrial, etc.). The estimated number of species ($\widehat{\text{TAXA}}$ or $\hat{\text{T}}$) is determined and the observed species value (TAXA or T) is then compared to the predicted value in ratio form ($T/\hat{T}$ or $TAXA/\widehat{TAXA}$). Comparisons of ratios between samples therefore reflects relative differences in diversity.

In order to examine the assumed accuracy in the behavior of this mathematical model, I determined the $T/\hat{T}$ value for several samples (see Chapter 5 for details on samples) and compared these values to another index that measures species richness (i.e. alpha value of Fisher et al. 1943). Basically, the alpha value is determined directly from a standardized chart given knowledge of the sample NISP and TAXA (Fisher et al. 1943). The raw data for each of these samples including the $T/\hat{T}$ and alpha values are shown in Table 12.

Since both the Fisher et al. (1943) alpha value and the $T/\hat{T}$ value presented here purport to measure species richness while accounting for sample size variation, the two estimates should vary in a similar manner. Figure 9 illustrates the behavior of these two indices for the Black Earth site samples. Similarly, Figures 10 and 11 illustrate the behavior of these indices for the Hall Shelter and Gordon II site samples, respectively. As is evident in these illustrations, the diversity trends for the two measures parallel each other. Apparent differences in magnitude are simply artifacts of scale position. Occasional deviations in trend direction, reflect the inadequacies of the Fisher et al. (1943) index, since that

Table 12. Raw data on sample size (NISP), number of observed taxa (TAXA), estimated number of taxa ($\widehat{\text{TAXA}}$), Fisher et al. (1943) diversity index value (ALPHA), and this study's diversity index value ($T/\hat{T}$), for samples from the Black Earth site, the Hall Shelter site and the Gordon II site. ($\hat{T}$ value calculated using the equation for Quaternary terrestrial snails in North America)

BLACK EARTH SITE

ZONE	NISP	TAXA	$\widehat{\text{TAXA}}$	$T/\hat{T}$	ALPHA
I	17	7	5.08	1.38	+6
II	298	20	17.51	1.14	4.8
IIIA	459	14	21.10	0.66	2.7
IIIB	263	15	16.59	0.90	3.5
IIIC	213	9	15.14	0.59	1.9
IIID	3	2	2.40	0.83	?

HALL SHELTER SITE

ZONE	NISP	TAXA	$\widehat{\text{TAXA}}$	$T/\hat{T}$	ALPHA
I	39	10	7.27	1.38	4.7
II	61	9	8.82	1.02	3.0
III	79	6	9.86	0.61	1.5
IVA	161	10	13.42	0.74	3.7
IVB	231	19	15.68	1.21	5.0

GORDON II SITE

LEVEL	NISP	TAXA	$\widehat{\text{TAXA}}$	$T/\hat{T}$	ALPHA
1	979	19	29.27	0.65	3.4
2	2540	23	44.18	0.52	3.5
3	1876	26	38.76	0.67	4.3
4	305	16	17.68	0.90	3.7

Figure 9. Diagram illustrating changes in snail diversity through time at the Black Earth site, using the Fisher et al. (1943) technique and the $T/\hat{T}$ technique.

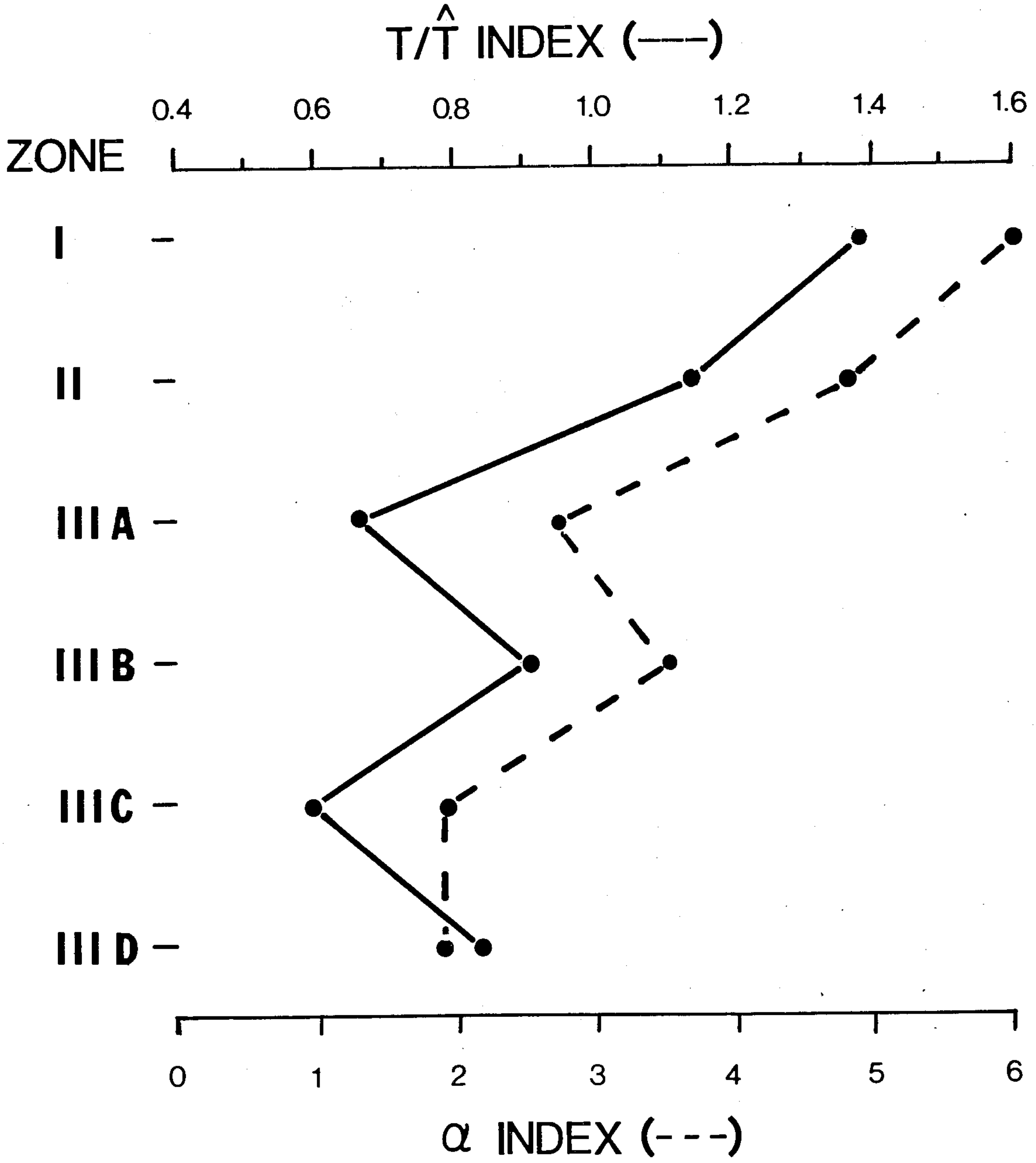

T/T̂ INDEX (——)
0.4
0.6
0.8
1.0
1.2
1.4
1.6
ZONE
I
II
III A
III B
III C
III D
0
1
2
3
4
5
6
α INDEX (- - -)

Figure 10. Diagram illustrating changes in snail diversity through time at the Hall Shelter, using the Fisher et al. (1943) technique and the $T/\hat{T}$ technique.

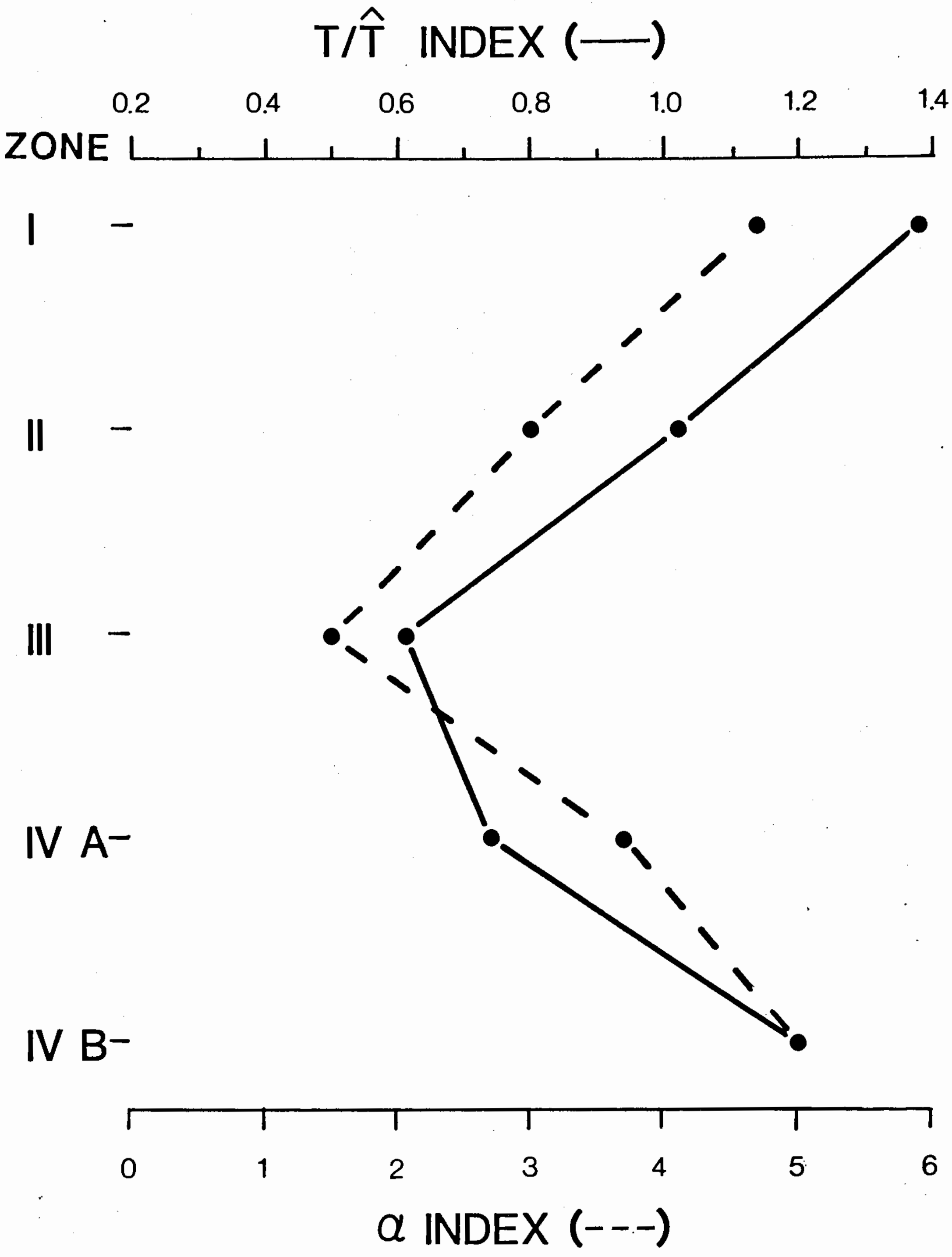
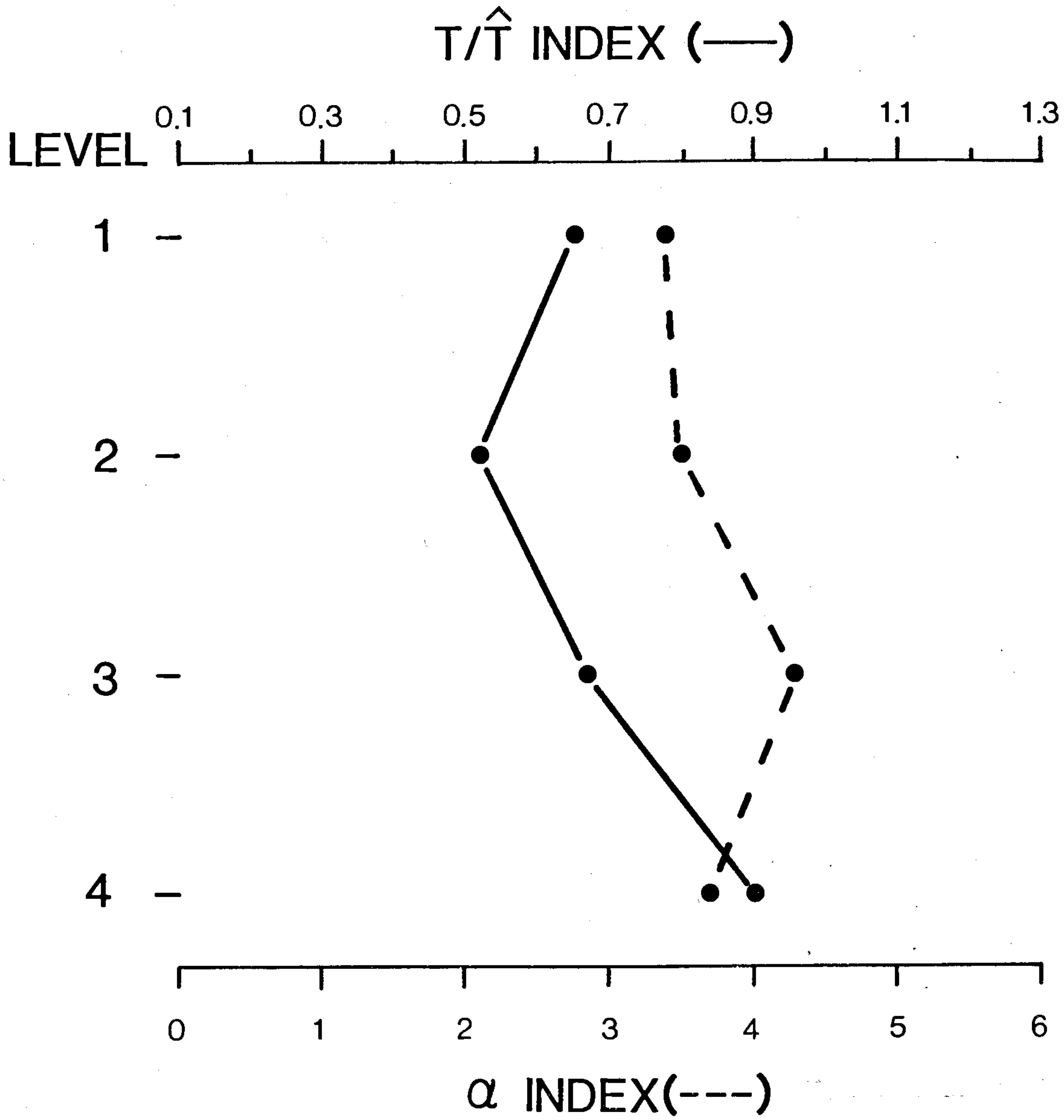

T/T̂ INDEX (——)
0.2
0.4
0.6
0.8
1.0
1.2
1.4
ZONE
I
II
III
IV A
IV B
0
1
2
3
4
5
6
α INDEX (---)

Figure 11. Diagram illustrating changes in snail diversity through time at the Gordon II site, using the Fisher et al. (1943) technique and the $T/\hat{T}$ technique.


T/T̂ INDEX (——)
LEVEL
0.1
0.3
0.5
0.7
0.9
1.1
1.3
1
2
3
4
0
1
2
3
4
5
6
α INDEX(---)

index is purely theoretical and the $T/\hat{T}$ index is empirically derived and specifically characteristic of gastropod assemblages, the latter is more appropriate. The $T/\hat{T}$ measure ensures that the primary assumptions for application of analysis are satisfied.

Application of this diversity measure in the interpretation of gastropod assemblages is presented in Chapter 5. As indicated in the discussions of site samples in Chapter 5, fluctuations in diversity lend insight into both cultural and natural environmental perturbations that have occurred in the past at specific locales.

Summary

Once retrieved, gastropods can be examined within a quantitative approach to derive useful information on shifting or stable diversity patterns. Diversity was shown to be a functionally applicable concept for understanding gastropod distribution in terms of limiting factors. As illustrated in this study, published primary data permit one to indicate major biological and climatic patterns through simple regression analysis. Collectively, the topics discussed in this and the previous chapter, provide ample evidence in opposition to the assumed belief that statistics play no role in molluscan zooarchaeology.

5. Gastropod Analysis

The purpose of the following discourse is threefold. First, I intend to explore the interpretive potentials of non-marine gastropod remains associated with several archaeological deposits. Second, I intend to show how a quantitative approach to gastropod analysis can augment classical qualitative research. Finally, to illustrate inter-site variability, the case studies under discussion derive from a wide range of archaeological situations.

My reasons for pursuing the above three aims are: 1) a presentation of empirical evidence adds substantial credence to any theoretical propositions; 2) since archaeological sites assume many forms, it logically follows that the potential uses of contained gastropod remains should also vary considerably, and that this variability should be examined and defined; and 3) the overt absence of quantitative research in molluscan studies, as practised by archaeologists, can only be rectified by practical illustrations.

The assemblages under examination were obtained from the Old Crow Basin, Yukon Territory, the Black Earth site, Illinois, and the Gordon II and Hall Shelter sites in Kentucky (Figure 1). Temporally, these assemblages vary from Late Pleistocene, to Archaic, Woodland, and Mississippian contexts.

Methodology

Details on sample location and recovery techniques employed for each of the sites are given under the separate site sample discussions. The Old Crow Basin samples were collected by Dr. Nat Rutter (Department of Geology, University of Alberta) and Mr. Tom Andrews (Department of Anthropology, University of Alberta). Collection of the Black Earth site samples was performed under the supervision of Dr. Richard Jefferies (Center for Archaeological Investigations, Southern Illinois University). The samples from the Hall Shelter site were collected by Mr. Tom Gatus (Department of Anthropology, University of Kentucky, Lexington). Samples from the Gordon II site were collected by the author.

Except for the Hall Shelter site samples, the remainder of the samples examined in this study were sieved through a minimum 0.5 mm sieve. Samples from the Hall Shelter site were sieved through 1.0 mm mesh sieves. All identifications were made under a 10x magnification using a binocular microscope with an occular micrometer. Taxonomic identifications were made by reference to various published keys and a comparative collection on loan from the Museum of Natural Sciences, National Museums of Canada, Ottawa. Representative specimens were then verified by either Mr. Jim van Es (Department of Zoology, University of Alberta) or Dr. Leslie Hubricht (Meridian, Mississippi). Taxonomic nomenclature employed in this study follows parts of Burch (1962, 1979), Clarke (1973, 1981), La Rocque (1967, 1968, 1970), Pilsbry (1940, 1946, 1948), and Taylor and Sohl (1962).

Ecological interpretations for each of the samples in the following syntheses represent abstractions of the detailed ecological requirements given in Appendix V. Interpretations of sample species richness and abundance distributions follow the theoretical and methodological reasonings outlined in Chapters two, three and four.

Background Discussion

Recent interdisciplinary studies in the Old Crow Basin, Yukon Territory, have shown that this area formed the eastern portion of the larger Berinigian refugium during much of the Quaternary (Ager 1976; Matthews 1976; Schweger and Habgood 1976; Stanley 1980). Further, archaeological investigations in the area have proven to be successful in showing evidence of early peopling into the New World (Irving 1976, 1978; Irving and Harington 1973; Morlan 1978; Morlan and Matthews 1978). Indeed, certain archaeologists contend that human occupation in the area may have begun over 50,000 years ago (Stanford et al. 1981).

If, in fact, the area was inhabited during much of the Late Pleistocene, an adequate interpretation of the paleoenvironmental conditions is essential in understanding early human migrations and man/land relations (Hopkins 1976). To this end, attention has been directed towards documenting and clarifying Pleistocene vertebrate communities (Crossman and Harington 1970; Harington 1977, 1980; Hoffman 1980; McAllister and Harington 1969; Repenning 1980), vegetational communities (Cwynar and Ritchie 1980; Schweger 1979) and surficial geology of the region (Hughes 1969, 1972; Morlan and Matthews 1978).

Unfortunately, only marginal thought has been given to the Quaternary molluscan fauna from the northern Yukon Territory (Bobrowsky 1980b; Clarke and Harington 1978; Delorme 1968; Delorme et al. 1977, 1978; Harington 1977). Given this paucity of molluscan data, several gastropod samples were obtained from the Old Crow Basin. These samples provide an initial base for supplementing paleoenvironmental interpretations of the Old Crow Basin.

Previous neontological and paleontological work on gastropods in the area includes research by Aubut (1978), Baker (1904, 1934), Bobrowsky (1980b), Clarke (1973, 1981), Clarke and Harington (1978), Dall (1905, 1917, 1919), Delorme et al. (1977, 1978), Hanna (1956), Harington (1977), and Whiteaves (1905). Additional pertinent information on molluscs from adjacent areas can be found in Brooks (1950), Henderson (1927), McCulloch et al. (1965), Sterki (1916), Tuthill (1963b), Tuthill and Johnson (1969), and Zhadin (1952).

Archaeological investigations by the Center for

Archaeological Investigations in the Carrier Mills Archaeological District, resulted in the discovery of a large deeply stratified site dating to the Middle Archaic. Excavations at the Black Earth site (11Sa87), Saline County, Illinois, indicated that the prehistoric locus consists of three large midden areas, with human occupation beginning approximately 5900 years ago (Jefferies 1980).

Excavation of midden Area A has resulted in a large sample of biological and cultural materials (see Jefferies 1980; Jefferies and Lynch 1980 for details). Given the excellent state of preservation for the recovered materials, the early age of the deposits, and the informative interpretations of prehistoric behavior, a column sample was obtained and examined for gastropods with the aim of explicating both the paleoenvironmental and cultural conditions at the site.

Previous research on gastropods in the state of Illinois is limited, but does include work by Baker (1923, 1930, 1931, 1936, 1939), Fowler and Parmalee (1959), Hubricht (1964c, 1972a), La Rocque (1963a, 1963b, 1964a, 1964b, 1966, 1967, 1968, 1970), Leonard (1972a, 1972b, 1974), Leonard and Frye (1960), Matteson (1953b), Parmalee (1967, 1968, 1969), Riggle (1976), and Schoenbeck (1939). Useful ancillary records and information on gastropods from neighboring states includes the work of Baerreis (1969, 1971), Black (1933), Brose (1972), Call (1900), Dawley (1955), Dexter (1953), Frye and Leonard (1952), Leonard (1950, 1952, 1959), Mead (1978), Miller (1964, 1966, 1968, 1970, 1975), Pauken (1969, 1971), Reynolds (1959), Semken et al. (1964), Tuthill (1961, 1963a,1967a), Tuthill and Laird (1963, 1964), Tuthill et al. (1964), Wayne (1959a), and Wootton (1975), as well as the following studies itemized in the Kentucky discussion.

To further document the potential variability involved in archaeological gastropod assemblage interpretation, samples were obtained from two sites in Kentucky. Samples from the Gordon II site, Livingston County, Kentucky, exemplify a case in which the sediments are of Mississippian age. As yet, no detailed archaeological studies have been attempted at the site, but a preliminary assessment by J. Nance indicates the site can be dated to post A.D. 900 (Nance personal communication).

Samples were obtained from the Hall Shelter site (15Pe8), Perry County, Kentucky, in an attempt to document the potentials and limitations of gastropod analysis in high altitude, rock shelter conditions. The gastropod assemblages from this site provide insight into both cave environments and cultural occupation patterns for the period covering the Late Archaic to the Late Prehistoric (Gatus 1981).

Analysis of the Kentucky samples was greatly facilitated by the ample body of existing information on gastropods. Previous work on gastropods in the areas includes the research of Baker (1928), Bickel (1967), Branson (1970), Branson and Batch (1969, 1971), Brown and Bruder (1963), Brown and McDonald (1960), Clench (1926), Conkin (1957), Goodrich (1934a, 1934b, 1934c, 1935, 1940, 1941), Hubricht (1960, 1964a, 1964b, 1968, 1972a, 1975), Kaplan and Minckley (1960), La Rocque (1963a, 1963b, 1964a, 1964b, 1966, 1967, 1968, 1970), Price (1900), Rosewater (1959), Taylor et al. (1977), and Vagvolgyi (1968). Additional pertinent information on distributional records for molluscs adjacent to Kentucky includes the research of Baker (1928), Bickel (1968), Burch (1955, 1956, 1957, 1962), Danglade (1922), Hubricht (1952, 1961, 1971, 1972b, 1976, 1979), La Rocque (1959), La Rocque and Conley (1956), La Rocque and Forsyth (1957), Leonard (1959), Miles and Reeder (1969), Pilsbry (1940, 1946, 1948), Reeder and Miles (1976), Rehder (1949), Robison (1978), Walter (1972), and Zimmerman (1960), as well as those references listed under the Illinois sample discussion.

Old Crow Basin

Gastropod samples were collected from Quaternary exposures along the Old Crow River, Yukon Territory, at four localities (Figure 1). Details on the exposure locations, associated material remains, and interpreted stratigraphy appear in Clarke and Harington (1978), Harington (1977, 1980), and Morlan and Matthews (1978). This study follows the stratigraphic synthesis and terminology outlined by Morlan and Matthews (1978).

A total of 20 gastropod samples from six major stratigraphic units were examined from the four localities. Table 13 provides the provenience of each of these samples according to the major units. The divisions of Units 4 and 6 into upper and lower components is of secondary stratigraphical importance. A total of 1966 specimens representing 14 taxa were recovered and identified in the 20 samples. Table 14 provides a systematic list of the gastropod taxa identified. In the discussion that follows, sample interpretations at each locality proceed in a chronological order beginning with the oldest.

i) Locality 11

Six samples were retrieved and examined for gastropods from locality 11. The frequency distributions for the taxa are given in Table 15.

Samples 8 and 9 from this locality are correlated with Unit 3A of the composite section. Both assemblages are dominated by A. limosa and V. s. helicoidea. These two species indicate that slow moving streams or eutrophic lake conditions prevailed at this locality during the time of unit deposition. Rich aquatic vegetation was probably present, and the mean annual temperature of the water may have been near 7.0

Table 13. Provenience of gastropod samples by localities from the Old Crow Basin, Yukon Territory, following Morlan and Matthews' (1978) classification scheme.

MORLAN/MATTHEWS COMPOSITE UNITS	LOCALITIES			
	11	12	15	44
6 (upper)	6U			
6 (lower)	6L			
4 (upper)		4U1		4U2
4 (lower)		2,4	4L	
3c		3c,6	3c1	
3b	10,11	3b,3	3b1	
3a	8,9	5		3a
2				2a

Table 14. Systematic list of gastropod taxa identified in Quaternary deposits from the Old Crow Basin, Yukon Territory.

Subclass: Prosobranchia
Order: Mesogastropoda

Family: Valvatidae
Valvata sincera helicoidea
Valvata piligera yukonensis
Valvata tricarinata

Family: Hydrobiidae
Amnicola limosa

Subclass: Pulmonata
Order: Basommatophora

Family: Lymnaeidae
Fossaria parva
Stagnicola catascopium
Stagnicola arctica
Stagnicola elodes
Stagnicola sp.

Family: Physidae
Physa jennessi
Physa sp.

Family: Planorbidae
Gyraulus circumstriatus
Gyraulus deflectus
Helisoma sp.

Table 15. Frequency distribution of gastropod taxa identified in samples from Locality 11, Old Crow Basin, Yukon Territory.

	SAMPLES						
TAXA	6U	6L	10	11	8	9	SUM
Valvata sincera helicoidea				3	10	21	34
Valvata piligera yukonensis		1				2	3
Amnicola limosa			5	2	24	207	238
Fossaria parva				1	4	2	7
Physa jennessi	1						1
Gyraulus circumstriatus	4						4
Gyraulus deflectus	2						2
TOTAL NISP	7	1	5	6	38	232	295

°C. Minor representation by *V. p. yukonensis* and *F. parva* in these samples is consistent with such an interpretation.

Samples 10 and 11 from this locality are correlated with Unit 3B of the composite section. The rank order of abundance for the taxa is identical to that observed in samples 8 and 9. Given the above, conditions are assumed to have been similar in both units.

Samples 6L and 6U from locality 11 represent Unit 6 of the composite section. The notable presence of *G. circumstriatus* and *P. jennessi* in these samples, as well as their respective modern ecological requirements, lends support to an interpretation that cool conditions prevailed at this locality during the Late Pleistocene.

ii) Locality 12

A total of eight samples, containing 612 identifiable specimens and representing five taxa, were examined from this locality (Table 16). The oldest unit at this locality (Unit 3A) is represented by one sample (sample 5). Sample 5 is dominated by *A. limosa* and *V. s. helicoidea*. A single specimen of *F. parva* was also retrieved from this sample. The two dominant taxa indicate that slow moving streams or eutrophic lake conditions prevailed in the area during the time of deposition. An abundance of aquatic vegetation may have been present. In all respects, this interpretation is

Table 16. Frequency distribution of gastropod taxa identified in samples from Locality 12, Old Crow Basin, Yukon Territory.

	SAMPLES								
TAXA	4U1	2	4	3c	6	3b	3	5	SUM
Valvata sincera helicoidea		34	5		12		48	13	112
Valvata piligera yukonensis	2			31		35			68
Amnicola limosa						89	200	141	430
Fossaria parva								1	1
Stagnicola elodes				1					1
TOTAL NISP	2	34	5	32	12	124	248	155	612

identical to that postulated for Unit 3A at locality 11.

Samples 3 and 3b from locality 12 are correlated with Unit 3B of the composite section. Collectively, the samples are dominated by the species *A. limosa*, *V. s. helicoidea*, and *V. p. yukonensis*. Conditions at this time appear to have consisted of slow moving streams and eutrophic lakes; both of which may have contained abundant aquatic vegetation. Overall, these interpretations suggest that conditions were similar to those in the preceding unit. Similarly, these environmental conditions posited for Unit 3B at locality 12 mimic those suggested for Unit 3B at locality 11.

Unit 3C of the composite section is represented at locality 12 by samples 6 and 3c. Collectively, the samples contain specimens of *V. p. yukonensis*, *V. s. helicoidea*, and *S. elodes*. The known ecological requirements of these taxa suggest that environmental conditions were periglacial in character; regionally cooler, with a landscape interspersed with muskeg pools. Most of these ponded situations were probably thick with northern aquatic vegetation; while the larger lakes ranged in character from oligotrophic to eutrophic.

Unit 4 of the composite section is represented by samples 2, 4, and 4U1 at locality 12. Only two gastropod taxa were identified in the samples. Ecologically, both *V. s. helicoidea* and *V. p. yukonensis* imply periglacial conditions prevailed in the area during the period represented by Unit 4.

iii) Locality 15

A total of three samples, containing 786 specimens and representing 11 gastropod taxa were examined from locality 15 (Table 17). Sample 3b1 from this locality is correlated with Unit 3B of the composite section. Only one specimen of *V. p. yukonensis* was retrieved in the sample. This taxonomic occurrence is not unusual given the presence of the species in sample 3b, Unit 3B, at locality 12.

Unit 3C of the composite section is represented by sample 3c1 at locality 15. Two species, *V. s. helicoidea* and *G. circumstriatus*, were identified in the sample. The present day ecological requirements of these taxa suggests that conditions at the time of deposition reflected a periglacial environment. An abundance of small muskeg ponds and pools probably existed in the area. A number of these water bodies maintained mud and silt substrates. This interpretation is identical to that proposed for Unit 3C at locality 12.

Sample 4L from locality 12 is correlated with Unit 4 of the composite section. A total of 756 specimens representing 13 taxa were recovered in this sample (Table 17). The three most abundant taxa are *V. s. helicoidea*, *G. circumstriatus*, and *G. deflectus*. Modern ecological requirements for these taxa suggests a large number of permanent water bodies existed

Table 17. Frequency distribution of gastropod taxa identified in samples from Locality 15, Old Crow Basin, Yukon Territory.

TAXA	SAMPLES 4L	 3c1	 3b1	 SUM
Valvata sincera helicoidea	655	27		682
Valvata piligera yukonensis	1		1	2
Valvata tricarinata	2			2
Fossaria parva	3			3
Stagnicola catascopium	1			1
Stagnicola arctica	1			1
Stagnicola sp.	15			15
Physa jennessi	16			16
Physa sp.	15			15
Gyraulus circumstriatus	22	2		24
Gyraulus deflectus	25			25
TOTAL NISP	756	29	1	786

in the area; ranging in character from oligotrophic lakes to vernal pools. Additionally, many of the ponds and pools probably contained an abundance of organics and aquatic plants. A very cool suite of habitats are proposed to have existed during this period given the presence of such northern forms in the sample as P. jennessi, S. arctica, and S. catascopium. In other words, the inferred environmental conditions were identical to those proposed for Unit 4 at locality 12.

iv) Locality 44

Three samples were retrieved and examined for gastropods from locality 44. The species identified and their respective frequencies are listed in Table 18. Sample 2a, correlated with Unit 2 of the composite section represents the oldest gastropod sample known from the Old Crow Basin. The presence of A. limosa in this sample indicates eutrophic lake habitats prevailed; a conclusion that agrees well with the sedimentological evidence that defines the unit as reworked lacustrine sediments (Morlan and Matthews 1978).

Unit 3A at locality 44 is represented by sample 3A. The dominant taxon in this sample is A. limosa, while intermediate taxa include V. s. helicoidea and V. p. yukonensis. Given this type of assemblage composition, conditions at the time of sediment deposition consisted of slow moving streams and eutrophic lakes. Both aquatic habitats were probably replete

Table 18. Frequency distribution of gastropod taxa identified in samples from Locality 44, Old Crow Basin, Yukon Territory.

	SAMPLES			
TAXA	4U2	3a	2a	SUM
Valvata sincera helicoidea	53	13		66
Valvata piligera yukonensis		9		9
Amnicola limosa		195	3	198
TOTAL NISP	53	217	3	273

with organics and vegetation. Basically, these conditions mimic those proposed for Unit 3A at localities 11 and 12.

The final sample (sample 4U2) from locality 44 is correlated with Unit 4 of the composite section. This monotypic assemblage contains 53 specimens of V. s. helicoidea. As with the case of the Unit 4 assemblage at locality 12, the inferred environment is one of slow streams and muskeg pools.

v) Summary

In general there is an excellent comparability between paleoenvironmental interpretations among the various localities and depositional units. The postulated environmental changes among units also appear to show an orderly succession. The glaciclacustrine clays of Unit 2 and the contained gastropod fauna indicate warm and strongly eutrophic lake habitats. Recovered species in the sandy sediments of Unit 3A also reflect eutrophic lakes, and slow moving streams rich in organics prevailed in the area. This environmental condition continues into the younger Unit 3B period.

Gastropods recovered from the cryoturbated organic silts of Unit 3C suggest a cooling in the general habitat to a more periglacial state. This condition is further emphasized in the succeeding Unit 4 samples, where a periglacial environment topographically dominated by muskeg pools is postulated.

Finally, the gastropod samples of Unit 6 suggest a very cold environment consisting of oligotrophic lakes characterized the interval. This interpretation conforms well to the postulated Late Wisconsin age for the Unit (Morlan and Matthews 1978).

Black Earth site

The Black Earth site (11Sa87), Saline County, Illinois, is a stratified Middle Archaic site located on a low upland area, adjacent to the South Fork of the Saline River (Figure 1). Details on site location, recovered archaeological materials, and inferred cultural chronology for the site are given by Jefferies (1980), and Jefferies and Lynch (1980).

Bulk samples measuring 25 x 25 x 10 cm were retrieved at 10 cm intervals from midden Area A, as part of a complete column. These samples, numbered 1 through 14, represent a complete history of deposition at the site starting at a depth of 140 cm below surface. This lower most level has been dated to ca. 5900 y.b.p. (Jefferies 1980).

Level 1 and 2 samples collected from the plow zone were grouped in the field prior to analysis. Levels 3 through 14 inclusive, therefore represent 10 cm intervals beginning at a depth of 30 cm below surface, and continuing down to a depth of 140 cm below surface. These 13 samples were then processed in the laboratory at Southern Illinois University using fine sieves and chemical flotation (Jefferies personal communication). Processing in the laboratory resulted in two convenient categories: heavy and light fractions. Heavy fractions represent those specimen remains retained in the 0.5 mm sieves in the bottom flot. Light fractions represent those specimens recovered in 2.0 and 0.5 mm mesh sieves employed on floating materials. Hand sorting of the above materials resulted in a total of 44 individual vials containing variable numbers of gastropod shells.

Sample fractions from the individual vials were sorted by hand under a binocular microscope. A total of 1253 gastropod specimens representing 30 taxa were identified in the sample fractions. Table 19 provides a systematic list of the species recovered in the samples.

The frequency distribution for identified taxa in the heavy fraction is given in Table 20. Similarly, the frequency distribution for identified taxa in the light fraction is given in Table 21. As is evident in these tabulations, 33.3% (n=10) of the total taxa were not recovered in the heavy fraction. A more positive recovery rate is shown by the light fraction results in which only 20% (n=6) of the total taxa were not recovered.

In terms of NISP recovery, the light fraction failed to recover 16.4% (n=206) of the total site NISP of 1253 (Table 22). In reality, these losses are not critical, since five of the six taxa not recovered in the light fraction represent

Table 19. Systematic list of gastropod taxa identified from the Black Earth site (11Sa87), Saline County, Illinois.

Subclass: Pulmonata
Order: Basommatophora

Family: Physidae
- *Helisoma trivolvis*

Order: Stylommatophora

Family: Polygyridae
- *Polygyra* sp.
- *Mesodon* sp.

Family: Zonitidae
- *Euconulus fulvus*
- *Euconulus chersinus*
- *Euconulus* sp.
- *Nesovitrea binneyana*
- *Retinella indentata*
- *Retinella* sp.
- *Mesomphix* cf. *vulgatus*
- *Mesomphix* sp.
- *Paravitrea* cf. *capsella*
- *Hawaiia minuscula*
- *Ventridens* sp.
- *Zonitoides arboreus*
- *Zonitoides* sp.

Family: Endodontidae
- *Anguispira alternata*
- *Anguispira kochi*
- *Discus* sp.
- *Helicodiscus parallelus*

Family: Strobilopsidae
- *Strobilops aenea*
- *Strobilops* sp.

Family: Pupillidae
- *Gastrocopta armifera*
- *Gastrocopta contracta*
- *Gastrocopta pentodon*
- *Gastrocopta corticaria*
- *Gastrocopta procera*
- *Pupoides albilabris*
- *Vertigo tridentata*
- gen. et. sp. indet.

Table 20. Frequency distribution of gastropod taxa identified in heavy fraction by excavation level from the Black Earth site (11Sa87).

	EXCAVATION LEVEL													
TAXA	1	3	4	5	6	7	8	9	10	11	12	13	14	SUM
Helisoma trivolvis						1								1
Euconulus fulvus				2										2
Euconulus chersinus			1											1
Nesovitrea binneyana					1				1					2
Retinella indentata			1								1			2
Mesodon sp.					1									1
Mesomphix cf. *vulgatus*			1											1
Mesomphix sp.								2	1					3
Paravitrea cf. *capsella*		1												1
Hawaiia minuscula			21	5	4	2		2	5	2	10	18		69
Ventridens sp.									1					1
Zonitoides arboreus			18	2	4			3	1	3	4	16	1	52
Anguispira alternata	1		15	1	8	2		3	4					34
Anguispira kochi		1	2		2	2	4							11
Helicodiscus parallelus			4		1									5
Strobilops aenea			1											1
Strobilops sp.					1									1
Gastrocopta armifera			4					2	1					7
Gastrocopta contracta			8									1		9
Pupillidae										1	1			2
TOTAL NISP	1	2	76	10	22	7	4	12	14	6	16	35	1	206
TOTAL TAXA	1	2	11	4	8	4	1	5	7	3	4	3	1	20

Table 21. Frequency distribution of gastropod taxa identified in light fraction by excavation level from the Black Earth site (11Sa87).

	EXCAVATION LEVEL													
TAXA	1	3	4	5	6	7	8	9	10	11	12	13	14	SUM
Polygyra sp.						1								1
Mesodon sp.		5												5
Euconulus fulvus		4	3	2	4	1	3	1	2	1				21
Euconulus sp.	1									1				2
Nesovitrea binneyana			1											1
Retinella indentata	1						1							2
Retinella sp.									2					2
Hawaiia minuscula	10	81	26	73	104	161	90	36	71	88	16	35	2	793
Zonitoides arboreus	1	19			7	5		1	1	10				44
Zonitoides sp.										1				1
Anguispira alternata		9	2	10	5	4	1	4	3	2				40
Anguispira kochi							1							1
Discus sp.		1												1
Helicodiscus parallelus		9	5			2								16
Strobilops aenea			1											1
Strobilops sp.						1								1
Gastrocopta armifera				6		4								10
Gastrocopta contracta		37	7	5	7	11	4	4		1				76
Gastrocopta pentodon			3		2	3								9
Gastrocopta corticaria			1											1
Gastrocopta procera	1													1
Pupoides albilabris	2													2
Vertigo tridentata		2					1	1						4
Pupillidae		3			2	1		2	3	1				12
TOTAL NISP	16	173	47	96	131	194	101	49	82	105	16	35	2	1047
TOTAL TAXA	6	11	9	5	7	11	7	7	6	8	1	1	1	24

Table 22. Frequency distribution and percent NISP not recovered in light fraction samples from the Black Earth site. (Measurements in millimeters from Burch 1962)

TAXA	TOTAL SITE NISP	LIGHT FRACTION NISP	% NISP NOT RECOVERED IN L.F.	MEAN WIDTH/ LENGTH
Helisoma trivolvis	1	0	100	
Polygyra sp.	1	1	0	
Mesodon sp.	6	5	17	?12
Euconulus fulvus	23	21	9	3.2
Euconulus chersinus	1	0	100	
Euconulus sp.	2	2	0	
Nesovitrea binneyana	3	1	67	3.8
Retinella indentata	4	2	50	5.9
Retinella sp.	2	2	0	
Mesomphix cf. *vulgatus*	1	0	100	
Mesomphix sp.	3	0	100	
Paravitrea cf. *capsella*	1	0	100	
Hawaiia minuscula	862	793	8	2.4
Ventridens sp.	1	0	100	
Zonitoides arboreus	96	44	54	5.5
Zonitoides sp.	1	0	100	
Anguispira alternata	74	40	46	2.2
Anguispira kochi	12	1	92	9.5
Discus sp.	1	1	0	
Helicodiscus parallelus	21	16	24	3.3
Strobilops aenea	2	1	50	2.6
Strobilops sp.	2	1	50	?2.6
Gastrocopta armifera	17	10	41	3.9
Gastrocopta contracta	85	76	11	2.3
Gastrocopta pentodon	9	9	0	
Gastrocopta corticaria	1	1	0	
Gastrocopta procera	1	1	0	
Pupoides albilabris	2	2	0	
Vertigo tridentata	4	4	0	
Pupillidae	14	12	14	?2.5
TOTAL NISP	1253	1047	16.4	
TOTAL TAXA	30	24	20.0	

single specimen occurrences. These taxa are therefore incidental forms in the assemblage, and are of minor importance in further ecological interpretations. Furthermore, 10 of the total taxa identified show a complete NISP recovery in the light fraction. This only leaves 14 taxa which show partial NISP recovery in the light fraction. Since most of these taxa are too large to float they would be expected to predominately occur in the bottom flot.

Relying on Burch's (1962) metrical data for gastropods, it is evident from Table 22 that the smallest taxon which shows any NISP loss in the light fraction has a mean length of approximately 2.3 mm. Furthermore, the NISP loss for this small taxon is a mere 11%. Of the 12 taxa which show greater than 10% NISP loss, eight have mean widths/lengths greater than 3.3 mm; again indicating a tendency for larger shells to be missed.

Gastropod specimens of this size would, therefore, appear in the bottom flot mesh. Since the use of flotation equipment implies data recovery maximization and time effort minimization, the above arguments are conistent with such an ideology (see Bobrowsky and Ball 1981). The use of fine sieves on floating materials maximize data retrieval, while coarse bottom sieves minimize time efforts. The frequencies from the heavy and light fractions can then be pooled to provide an accurate data base for further interpretations (Table 23).

Table 23. Frequency distribution of gastropod taxa identified in total samples by excavation level from the Black Earth site (11Sa87).

	EXCAVATION LEVEL													
TAXA	1	3	4	5	6	7	8	9	10	11	12	13	14	SUM
Helisoma trivolvis							1							1
Polygyra sp.						1								1
Mesodon sp.		5			1									6
Euconulus fulvus		4	3	4	4	1	3	1	2	1				23
Euconulus chersinus			1											1
Euconulus sp.	1									1				2
Nesovitrea binneyana			1		1				1					3
Retinella indentata	1		1				1				1			4
Retinella sp.									2					2
Mesomphix cf. *vulgatus*			1											1
Mesomphix sp.								2	1					3
Paravitrea cf. *capsella*		1												1
Hawaiia minuscula	10	81	47	78	108	163	90	38	76	90	26	53	2	862
Ventridens sp.									1					1
Zonitoides arboreus	1	19	18	2	11	5		4	2	13	4	16	1	96
Zonitoides sp.										1				1
Anguispira alternata	1	9	17	11	13	6	1	7	7	2				74
Anguispira kochi		1	2		2	2	5							12
Discus sp.		1												1
Helicodiscus parallelus		9	9		1	2								21
Strobilops aenea			2											2
Stobilops sp.					1	1								2
Gastrocopta armifera			4	6		4		2	1					17
Gastrocopta contracta		37	15	5	7	11	4	4		1		1		85
Gastrocopta pentodon		1	1		2	3								9
Gastrocopta corticaria			1											1

Table 23 (continued)

Gastrocopta procera	1													1
Pupoides albilabris	2													2
Vertigo tridentata		2					1	1						4
Pupillidae		3			2	1		2	3	2	1			14
TOTAL NISP	17	175	123	106	153	200	106	61	96	111	32	70	3	1253
TOTAL TAXA	7	13	15	6	12	12	8	9	10	8	4	3	2	30

The arbitrary excavation levels were then grouped into cultural zones; the latter defined archaeologically by Jefferies (1980). According to this zonation scheme, Zones IIID to IIIA represent early to late Middle Archaic occupation, Zone II represents Late Archaic to Middle Woodland occupation, while Zone I is the disturbed plow zone assemblage. By relying on the grouped frequency distributions (Table 24) by cultural zones and the modern ecological requirements of individual taxa (Appendix V), it is now possible to provide an interpretation of the local environmental and cultural conditions characterizing various occupation periods at the Black Earth site. In the discussion that follows, chronological interpretation beginning with the oldest is presented by cultural zone.

i) Zone IIID

The gastropod sample from this stratum represents the early Middle Archaic. Only three specimens representing two species were recovered and identified in this sample; namely, _H. minuscula_ and _Z. arboreus_. The reason for such a small sample size in light of controlled volumetric collection suggests: 1) antiquity of the deposit precludes adequate preservation; 2) environmental conditions at the time of deposition were unfavorable for gastropod habitation; or 3) the single sample representing recovered density and

Table 24. Total frequency distribution of gastropod taxa identified by arbitrary cultural strata/zones from the Black Earth site (11Sa87).

	CULTURAL ZONES						
TAXA	I	II	IIIA	IIIB	IIIC	IIID	SUM
Helisoma trivolvis				1			1
Polygyra sp.			1				1
Mesodon sp.		5	1				6
Euconulus fulvus		7	9	6	1		23
Euconulus chersinus		1					1
Euconulus sp.	1				1		2
Nesovitrea binneyana		1	1	1			3
Retinella indentata	1	1		1	1		4
Retinella sp.				2			2
Mesomphix cf. *vulgatus*		1					1
Mesomphix sp.				3			3
Paravitrea cf. *capsella*		1					1
Hawaiia minuscula	10	128	349	204	169	2	862
Ventridens sp.				1			1
Zonitoides arboreus	1	37	18	6	33	1	96
Zonitoides sp.					1		1
Anguispira alternata	1	26	30	15	2		74
Anguispira kochi		3	4	5			12
Discus sp.		1					1
Helicodiscus parallelus		18	3				21
Strobilops aenea		2					2
Strobilops sp.			2				2
Gastrocopta armifera		4	10	3			17
Gastrocopta contracta		52	23	8	2		85
Gastrocopta pentodon		4	5				9
Gastrocopta corticaria		1					1

Table 24 (continued)

Gastrocopta procera	1						1
Pupoides albilabris	2						2
Vertigo tridentata		2		2			4
Pupillidae		3	3	5	3		14
TOTAL NISP	17	298	459	263	213	3	1253
TOTAL TAXA	7	20	14	15	9	2	30

diversity is insufficient due to sampling, and fails to provide an adequate representation of molluscan taxonomic abundance. With the above considerations in mind, the diversity estimate illustrated for this sample in Figure 9 is obviously questionable.

Superficially, the two species identified in the sample tend to reflect local environmental conditions at a pioneering stage of community development. This suggestion follows from the calculated low diversity estimate. It also follows from the nature of the assemblage composition. Since both taxa are basically ubiquitous forms known to favor humus in wooded areas, it is possible that the immediate midden area was partially forested with aspen, while the midden itself was relatively clear due to periodic environmental perturbations in the form of river flooding.

ii) Zone IIIC

The gastropod sample from Zone IIIC is informative in several respects. Overall observed density of recovered specimens is greater than that of the preceding zone, but species richness remains relatively unchanged (Figure 9). These observations support the contention that the small sample in Zone IIID does in fact represent preservational biases. Furthermore, the stability in species richness between the two zones, as well as the similarity in community character, discount the possibility of sample biasing.

The dominant taxa in this sample remain H. minuscula and Z. arboreus. These species and incidental taxa such as E. fulvus, and A. alternata indicate conditions in the area were of a moist wooded nature. These species are commonly collected in floodplain margins or under humus and mosses in wooded areas. An ample amount of leaf mold and fallen logs existed in the area, with occasional breaks forming open woodland and grassland. Nearby streams and marshes must have existed in the vicinity of the midden, although not as a prominent terrain feature. The presence of G. contracta and R. indentata in the sample suggests nearby hillsides were also wooded. Even with the larger sample, it is evident that the gastropod community structure was still unstable as inferred in Zone IIID. Environmentally, conditions appear to have remained relatively similar to that of the preceding time interval.

iii) Zone IIIB

The specimen density for this sample is only marginally greater than that in Zone IIIC (Table 25). Species richness, however, shows a successional increase; a shift suggestive of gradual community stabilization (Figure 9). This suggestion is partially confirmed by several proportional increases in species such as E. fulvus, A. alternata, and G. contracta. Although H. minuscula remains the dominant element in the

Table 25. Proportional distribution of total gastropod taxa identified by arbitrary cultural strata/zones from the Black Earth site (11Sa87).

	CULTURAL ZONES						
TAXA	I	II	IIIA	IIIB	IIIC	IIID	SUM
Helisoma trivolvis				.004			.0008
Polygyra sp.			.002				.0008
Mesodon sp.		.017	.002				.0048
Euconulus fulvus		.023	.020	.023	.005		.0184
Euconulus chersinus		.003					.0008
Euconulus sp.	.059				.005		.0016
Nesovitrea binneyana		.003	.002	.004			.0024
Retinella indentata	.059	.003		.004	.005		.0032
Retinella sp.				.008			.0016
Mesomphix cf. *vulgatus*		.003					.0008
Mesomphix sp.				.011			.0024
Paravitrea cf. *capsella*		.003					.0008
Hawaiia minuscula	.588	.430	.760	.776	.793	.667	.6879
Ventridens sp.				.004			.0008
Zonitoides arboreus	.059	.124	.039	.023	.155	.333	.0766
Zonitoides sp.					.005		.0008
Anguispira alternata	.059	.087	.065	.057	.009		.0591
Anguispira kochi		.010	.009	.019			.0096
Discus sp.		.003					.0008
Helicodiscus parallelus		.060	.006				.0168
Strobilops aenea		.007					.0016
Strobilops sp.			.004				.0016
Gastrocopta armifera		.013	.022	.011			.0136
Gastrocopta contracta		.174	.050	.030	.009		.0678
Gastrocopta pentodon		.013	.011				.0072
Gastrocopta corticaria		.003					.0008

Table 25 (continued)

Gastrocopta procera	.059						.0008
Pupoides albilabris	.118						.0016
Vertigo tridentata		.007		.008			.0032
Pupillidae		.010	.006	.019	.014		.0112
TOTAL NISP	17	298	459	263	213	3	1253
TOTAL TAXA	7	20	14	15	9	2	30

assemblage, new incidental representation by N. binneyana, and A. kochi suggests increasing calcium accumulations at the locus. This calcium increase is documented pedologically and is assumed to be a result of increasing cultural activities (see Jefferies 1980).

Although a wooded environment still predominates, partial forest reduction and clearing in the area is suggested by the marked proportional reduction in Z. arboreus representation. Increased fluvial and lacustrine habitats in the midden vicinity is inferred by the novel occurrence of the freshwater species H. trivolvis, and floodplain fauna Ventridens sp., A. alternata, and G. armifera. Furthermore, increased local cooling (artificial?) is suggested by the presence of V. tridentata and Ventridens sp. in the sample.

iv) Zone IIIA

The gastropod assemblage from Zone IIIA shows the highest specimen density observed at the site (Table 25). Conversely, there is a notable drop in species richness (Figure 9). Both of these observations support Jefferies' (1980) contention that the period sampled represents a time of increased human activity.

First, the artificial increase in accumulated calcium at the site through increased burning activities (Jefferies and Lynch 1980) would attract a larger 'number' of gastropods, and not necessarily a greater variety. Second, increased human activities would favor synanthropic species such as *E. fulvus*, and *H. minuscula*; an hypothesis borne out by the frequency distributions. Third, a higher density of gastropods would reduce the amount of species packing and thus reduce the overall species richness. Fourth, an intensification in forest clearing activities at this time should have the effect of reducing the abundance of log obligatory taxa such as *Z. arboreus*; again, an hypothesis confirmed by the empirical observations. Finally, the sudden appearance of *G. pentodon* and *Strobilops* sp. in the assemblage supports the assumption that clearing occurred, since both taxa are obligatory to well drained grassland habitats.

In short, at the termination of the Middle Archaic (ca. 4900 y.b.p.) lake and riverine habitats were still present in the region, but with reduced roles in the environment. Areas in the immediate vicinity of the midden area tended towards open woodland and grassland, with reduced moisture and dampness; a natural environmental condition resulting from cultural stimuli.

v) Zone II

This assemblage represents the Late Archaic to Middle Woodland occupation at the site (Jefferies 1980). The exceptionally high molluscan diversity (Figure 9) reflected by this sample immediately suggests that the successional shift is one towards community maturation.

The sample from Zone II contains four dominant, one intermediate, and 15 recedent gastropod taxa. High representation by new taxa from a variety of habitats, as well as shifts in dominance and abundance of repetitive taxa, all point towards reduced human activity at the locus following the Middle Archaic.

Given the species composition of the assemblage, the environmental conditions probably resembled those which existed in Zones IIIC and IIIB. Forested areas were beyond the pioneer stage, and aquatic habitats stabilized to that now present in the area.

vi) Zone I

The gastropod sample from this zone represents the modern plow zone community. Species richness is lower than that of Zone II, but is still fairly high (Figure 9). Environmental instability due to annual plowing activities should have the result of lowering species diversity. Similarly, the sudden appearance of dry grassland taxa such as _P_. _albilabris_ and _G_. _procera_ into the assemblage supports the plow zone field observation. In several respects, this plow zone community behavior mimics the plow zone assemblage from the Gordon II site, Kentucky.

vii) Summary

The subfossil gastropod remains recovered from the Black Earth site, Illinois, provide an excellent data base for interpreting changing paleoenvironmental conditions at the site during the last 6000 years. Briefly, the oldest and second oldest assemblages from Zones IIID and IIIC indicate pioneering and transitional environs. The area was wooded, humid and thick with decaying humus, moss and other vegetation. During Zone IIIB there appears to have been a localized cooling, increase in humidity and successional move towards community maturation. Vegetatively, however, there are indications of initial localized clearing and deforestation. This deforestation appears to have reached a maximum during Zone IIIA, that is, near the termination of the Middle Archaic. Furthermore, cultural activity appears to have been most intensive during this time interval.

During the Late Archaic to Middle Woodland period, a period represented by the Zone II gastropod assemblage, there was a reversal in the successional trend. Natural forest and floodplain species indicate a return in conditions similar to that posited for Zone IIIC. Finally, the plow zone assemblage from Zone I chracterizes a dry grassland type of habitat, an environmental state now apparent at the site.

Gordon II site

The Gordon II site, Livingston County, Kentucky, is located on the south shore of the Ohio River, approximately 4.5 kilometers north of Bayou, Kentucky. Artifacts recovered by J. Nance suggest the site is Mississippian, and therefore postdates A.D. 900 (Nance personal communication). Two areas on the site were arbitrarily chosen for excavation. A one by one meter unit was excavated in each of the two areas. Unit one was located approximately 100 meters from the shores of an old back water channel pond. Unit two was located approximately 10 meters from the channel shoreline.

Each unit was excavated in arbitrary 10 cm levels; Levels 1 and 2 encompassed the entire plow zone. All of the excavated sediment was then wet sieved through 0.5 mm mesh sieves. The retained sieve fractions were then sorted by hand for shell identification. A total of 5700 gastropod specimens representing 35 taxa were recovered from the site. Table 26 itemizes the gastropod taxa identified from the Gordon II site samples. Table 27 provides the frequency distribution for gastropods identified in Unit One, while Table 28 provides the frequency distribution for gastropods identified in Unit Two.

Prior to interpreting the environmental shifts at the site as suggested by the presence of gastropod remains, a test of data comparability between the two units is necessary. This test will statistically illustrate whether or not the arbitrary

Table 26. Systematic list of gastropod taxa identified from the Gordon II site, Livingston County, Kentucky.

Subclass: Prosobranchia
Order: Mesogastropoda

Family: Viviparidae
- *Campeloma decisum*

Family: Valvatidae
- *Valvata bicarinata*

Family: Hydrobiidae
- *Amnicola limosa*

Family: Pleuroceridae
- *Pleurocera acutum*
- *Goniobasis livescens*

Subclass: Pulmonata
Order: Basommatophora

Family: Lymnaeidae
- *Stagnicola* cf. *elodes*

Family: Planorbidae
- *Gyraulus parvus*

Order: Stylommatophora

Family: Polygyridae
- *Triodopsis* sp.

Family: Zonitidae
- *Euconulus fulvus*
- *Euconulus chersinus*
- ?*Guppya* cf. *sterkii*
- *Nesovitrea binneyana*
- *Retinella wheatleyi*
- *Retinella indentata*
- *Mesomphix vulgatus*
- *Mesomphix friabilis*
- *Mesomphix* cf. *cupreus*
- *Mesomphix* sp.
- *Paravitrea* sp.
- *Hawaiia minuscula*
- *Ventridens demissus*
- *Zonitoides arboreus*

Table 26 (continued)

Family: Endodontidae
    Anguispira alternata
    Discus patulus
    Helicodiscus parallelus

Family: Succineidae
    Succinea cf. *grosvenori*
    Succinea cf. *avara*
    Succinea sp.

Family: Pupillidae
    Gastrocopta armifera
    Gastrocopta contracta
    Gastrocopta pentodon
    Gastrocopta procera
    Pupoides albilabris
    Vertigo tridentata
    gen. et. sp. indet.

Table 27. Frequency distribution of gastropod taxa identified in Unit One, by excavation level, from the Gordon II site.

TAXA	EXCAVATION LEVEL 1	2	3	4	SUM
Campeloma decisum	7	9	9	8	33
Valvata bicarinata		1			1
Amnicola limosa	11	21	14	2	48
Pleurocera acutum		1	1		2
Goniobasis livescens		1	3		4
Stagnicola cf. *elodes*	1				1
Gyraulus parvus			1		1
Triodopsis sp.				1	1
Euconulus fulvus	4	47	62		113
Gyppya cf. *sterkii*		1			1
Retinella indentata	3	5	11	1	20
Mesomphix vulgatus			1		1
Mesomphix friabilis		1			1
Mesomphix cf. *cupreus*				2	2
Mesomphix sp.	5		1		6
Paravitrea sp.				1	1
Hawaiia minuscula	158	452	369	95	1074
Ventridens demissus	1				1
Zonitoides arboreus	19	69	93	22	203
Anguispira alternata		3	3	1	7
Helicodiscus parallelus	4	10	10	6	30
Succinea cf. *grosvenori*	2				2
Succinea cf. *avara*	5				5
Succinea sp.		7	2		9
Gastrocopta armifera	17	87	180	2	286
Gastrocopta contracta	10	21	20	9	60
Gastrocopta pentodon		7	3		10
Gastrocopta procera		8	5		13
Pupoides albilabris	243	735	642	58	1678
Vertigo tridentata		1	1		2
Pupillidae		4	1		5
TOTAL NISP	490	1491	1432	208	3621
TOTAL TAXA	15	21	21	13	31

Table 28. Frequency distribution of gastropod taxa identified in Unit Two, by excavation level, from the Gordon II site.

TAXA	EXCAVATION LEVEL 1	2	3	4	SUM
Campeloma decisum			3	3	6
Valvata bicarinata				1	1
Amnicola limosa	16	19	9	2	46
Pleurocera acutum		2			2
Goniobasis livescens		2		1	3
Gyraulus parvus		1			1
Euconulus fulvus	13	41	4	4	62
Euconulus chersinus			1		1
Nesovitrea binneyana			1		1
Retinella wheatleyi			1		1
Retinella indentata	6	7	9	1	23
Mesomphix cf. *cupreus*		6	2		8
Hawaiia minuscula	81	70	167	35	353
Zonitoides arboreus	23	29	38	6	96
Anguispira alternata	5	12	1		18
Discus patulus			4		4
Helicodiscus parallelus	8	19	32	5	64
Succinea sp.	10	16	8		34
Gastrocopta armifera	25	86	23	8	142
Gastrocopta contracta	15	36	22	5	78
Gastrocopta procera	14	11	12		37
Pupoides albilabris	269	685	98	26	1052
Pupillidae	4	7	9		20
TOTAL NISP	489	1049	444	97	2053
TOTAL TAXA	13	17	19	12	23

excavation units and component samples reflect similar community species proportions. If the samples differ, the interpretation of individual units must also differ, thus creating the problem of determining which of the two unit assemblages is the more accurate sample. The only taxa worthy of consideration in this analysis are those species representing greater than three percent of the specimen abundance, that is, only intermediate and dominant fauna. Given this restriction, a G-test was performed between level sample pairs for the two units to determine if the proportion of dominant and intermediate taxa were significantly independent. Table 29 outlines the resultant analysis following the methodology of Sokal and Rohlf (1969).

As is evident from Table 29 each pair of levels provides a significant G-value at the 0.005 level of significance. In other words, one can conclude that the null hypothesis of statistical independence can be rejected, and that the proportions of intermediate and dominant taxa in each of the level pairs are similar in the two units.

Additionally, one wishes to examine the potential for variation in the ranked abundance of individual taxa in paired level samples. As in the previous test, if differences in the ranked abundance of taxa for the two units exist, an additional problem of determining the accurate samples is introduced. My intention is to show that there is little difference between

Table 29. R x C test of independence for level pairs from the Gordon II site using the G-test.

	LEVEL PAIRS			
	1	2	3	4
species (n)	6	6	7	8
degrees of freedom	5	5	6	7
G-value	29.48	243.28	167.25	23.20
significance level	0.005	0.005	0.005	0.005

the two unit samples. In this case, the measure of association between level pairs can be determined using the Spearman rank correlation test for tied observations following the methodology of Siegel (1956). Species common to one or both samples were included in the analysis, hence recedent taxa were also evaluated in the computations. Ranked abundance of the taxa was determined using the proportional values given in Tables 30 and 31. Table 32 outlines the results of the four tests on paired samples. As indicated in the tabulation, the rank order of abundance in the level pairs is significantly comparable at the 0.01 level of significance.

The above two tests indicate that there is no major variation in the ranked abundance and proportional representation of species in the paired levels of the two units. Given the results of the statistical analyses, data from level pairs were grouped for further consideration. Table 33 provides the frequency distribution for identified taxa in the pooled sample levels. Similarly, Table 34 gives the proportions of these taxa in the pooled samples.

As shown in Table 34 the NISP varies from a low of 305 in Level 4, to a high of 2540 for Level 2. The range of TAXA values varies from a low of 16 in Level 4 to a high of 26 in Level 3.

The significance of the observed variation in TAXA and NISP values from level to level is difficult to assess at face

Table 30. Proportional distribution of gastropod taxa identified in Unit One, by excavation level, from the Gordon II site.

	EXCAVATION LEVEL				
TAXA	1	2	3	4	SUM
Campeloma decisum	.014	.006	.006	.038	.0091
Valvata bicarinata		.001			.0003
Amnicola limosa	.022	.014	.010	.010	.0132
Pleurocera acutum		.001	.001		.0006
Goniobasis livescens		.001	.002		.0011
Stagnicola cf. *elodes*	.002				.0003
Gyraulus parvus			.001		.0003
Triodopsis sp.				.005	.0003
Euconulus fulvus	.008	.032	.043		.0312
Guppya cf. *sterkii*		.001			.0003
Retinella indentata	.006	.003	.008	.005	.0055
Mesomphix vulgatus			.001		.0003
Mesomphix friabilis		.001			.0003
Mesomphix cf. *cupreus*				.010	.0006
Mesomphix sp.	.010		.001		.0016
Paravitrea sp.				.005	.0003
Hawaiia minuscula	.322	.303	.258	.457	.2891
Ventridens demissus	.002				.0003
Zonitoides arboreus	.039	.046	.065	.106	.0561
Anguispira alternata		.002	.002	.005	.0019
Helicodiscus parallelus	.008	.007	.007	.029	.0083
Succinea cf. *grosvenori*	.004				.0006
Succinea cf. *avara*	.010				.0014
Succinea sp.		.005	.001		.0025
Gastrocopta armifera	.035	.058	.126	.010	.0790
Gastrocopta contracta	.020	.014	.014	.043	.0166
Gastrocopta pentodon		.005	.002		.0028
Gastrocopta procera		.005	.003		.0036
Pupoides albilabris	.496	.493	.448	.279	.4634
Vertigo tridentata		.001	.001		.0006
Pupillidae		.003	.001		.0014
TOTAL NISP	490	1491	1432	208	3621
TOTAL TAXA	15	21	21	13	31

Table 31. Proportional distribution of gastropod taxa identified in Unit Two, by excavation level, from the Gordon II site.

	EXCAVATION LEVEL				
TAXA	1	2	3	4	SUM
Campeloma decisum			.007	.031	.0029
Valvata bicarinata				.010	.0005
Amnicola limosa	.033	.018	.020	.021	.0224
Pleurocera acutum		.002			.0010
Goniobasis livescens		.002		.010	.0015
Gyraulus parvus		.001			.0005
Euconulus fulvus	.026	.039	.009	.041	.0302
Euconulus chersinus			.002		.0005
Nesovitrea binneyana			.002		.0005
Retinella wheatleyi			.002		.0005
Retinella indentata	.012	.007	.020	.010	.0112
Mesomphix cf. *cupreus*		.006	.004		.0039
Hawaiia minuscula	.166	.067	.376	.361	.1719
Zonitoides arboreus	.047	.028	.086	.062	.0468
Anguispira alternata	.010	.011	.002		.0088
Discus patulus			.009		.0019
Helicodiscus parallelus	.016	.018	.072	.052	.0312
Succinea sp.	.020	.015	.018		.0166
Gastrocopta armifera	.051	.082	.052	.082	.0692
Gastrocopta contracta	.031	.034	.050	.052	.0380
Gastrocopta procera	.029	.010	.027		.0180
Pupoides albilabris	.550	.653	.221	.268	.5124
Pupillidae	.008	.007	.020		.0097
TOTAL NISP	489	1049	444	97	2053
TOTAL TAXA	13	17	19	12	23

Table 32. Measure of association between level pairs from the Gordon II site using the Spearman rank correlation coefficient for tied observations.

	LEVEL PAIRS			
	1	2	3	4
species (n)	9	15	14	10
r_s	0.984	0.939	0.660	0.770
significance level	0.01	0.01	0.01	0.01

Table 33. Frequency distribution of gastropod taxa identified in total sample (Unit One and Unit Two) by excavation level from the Gordon II site.

	EXCAVATION LEVEL				
TAXA	1	2	3	4	SUM
Campeloma decisum	7	9	12	11	39
Valvata bicarinata		1		1	2
Amnicola limosa	27	40	23	4	94
Pleurocera acutum		3	1		4
Goniobasis livescens		3	3	1	7
Stagnicola cf. *elodes*	1				1
Gyraulus parvus		1	1		2
Triodopsis sp.				1	1
Euconulus fulvus	17	88	66	4	175
Euconulus chersinus			1		1
Guppya sterkii		1			1
Nesovitrea binneyana			1		1
Retinella wheatleyi			1		1
Retinella indentata	9	12	20	2	43
Mesomphix vulgatus			1		1
Mesomphix friabilis		1			1
Mesomphix cf. *cupreus*		6	2	2	10
Mesomphix sp.	5		1		6
Paravitrea sp.				1	1
Hawaiia minuscula	239	522	536	130	1427
Ventridens demissus	1				1
Zonitoides arboreus	42	98	131	28	299
Anguispira alternata	5	15	4	1	25
Discus patulus			4		4
Helicodiscus parallelus	12	29	42	11	94
Succinea cf. *grosvenori*	2				2
Succinea cf. *avara*	5				5
Succinea sp.	10	23	10		43
Gastrocopta armifera	42	173	203	10	428
Gastrocopta contracta	25	57	42	14	138
Gastrocopta pentodon		7	3		10
Gastrocopta procera	14	19	17		50
Pupoides albilabris	512	1420	740	84	2756
Vertigo tridentata		1	1		2
Pupillidae	4	11	10		25
TOTAL NISP	979	2540	1876	305	5700
TOTAL TAXA	19	23	26	16	35

Table 34. Proportional distribution of gastropod taxa identified in total sample (Unit One and Unit Two), by excavation level, from the Gordon II site.

	EXCAVATION LEVEL				
TAXA	1	2	3	4	SUM
Campeloma decisum	.007	.004	.006	.036	.0068
Valvata bicarinata		.001		.003	.0004
Amnicola limosa	.028	.016	.012	.013	.0165
Pleurocera acutum		.001	.001		.0007
Goniobasis livescens		.001	.002	.003	.0012
Stagnicola cf. *elodes*	.001				.0002
Gyraulus parvus		.001	.001		.0004
Triodopsis sp.				.003	.0002
Euconulus fulvus	.017	.035	.035	.013	.0307
Euconulus chersinus			.001		.0002
Guppya cf. *sterkii*		.001			.0002
Nesovitrea binneyana			.001		.0002
Retinella wheatleyi			.001		.0002
Retinella indentata	.009	.005	.011	.006	.0075
Mesomphix vulgatus			.001		.0002
Mesomphix friabilis		.001			.0002
Mesomphix cf. *cupreus*		.002	.001	.006	.0018
Mesomphix sp.	.005		.001		.0010
Paravitrea sp.				.003	.0002
Hawaiia minuscula	.244	.206	.286	.426	.2504
Ventridens demissus	.001				.0002
Zonitoides arboreus	.043	.038	.070	.092	.0524
Anguispira alternata	.005	.006	.002	.003	.0044
Discus patulus			.002		.0007
Helicodiscus parallelus	.012	.011	.022	.036	.0165
Succinea cf. *grosvenori*	.002				.0004
Succinea cf. *avara*	.005				.0009
Succinea sp.	.010	.009	.005		.0075
Gastrocopta armifera	.043	.068	.108	.033	.0751
Gastrocopta contracta	.026	.022	.022	.046	.0242
Gastrocopta pentodon		.003	.002		.0018
Gastrocopta procera	.014	.007	.009		.0088
Pupoides albilabris	.523	.559	.394	.275	.4835
Vertigo tridentata		.001	.001		.0004
Pupillidae	.004	.004	.005		.0044
TOTAL NISP	979	2540	1876	305	5700
TOTAL TAXA	19	23	26	16	35

value. To facilitate interpretation, I examined the variation in species richness by level. Table 12 provides the calculated variation in species richness for the four samples. Figure 11 illustrates the temporal fluctuations in species richness for the pooled samples using the data in Table 12. This quantitative data can be combined with the qualitative ecological data for the taxa (Appendix V) to furnish a basis for interpreting the paleoenvironmental conditions at the Gordon II site.

i) Level 4

The oldest sample from this site contains a very rich assemblage (Figure 11). This diverse sample contains three dominant, four intermediate, and 10 recedent taxa. The dominant fauna is primarily ubiquitous in character, suggestive of moist conditions in a mixed deciduous forest community. Intermediate taxa such as G. armifera, G. contracta, and C. decisum further emphasize poor drainage in the area, as well as the existence of nearby aquatic habitats. The high proportion of H. parallelus in this sample also indicates a damp habitat in a closed forested area.

The identified aquatics indicate that quiet and shallow water, rich in vegetation existed near the site. Conversely, the low proportions of such species as P. indentata and A. alternata, open area forms that favor drier conditions, further suggests that a moist, well-shaded wooded habitat prevailed in the site area.

ii) Level 3

The sample from Level 3 shows a slight reduction in species richness (Figure 11). There is a slight increase in the abundance of *P. albilabris*, *G. armifera*, and *R. indentata*. On the other hand, there is a reduction in the abundance of *M. cupreus*, *Z. arboreus*, and *H. parallelus*.

The observed shifts in abundance suggest a reduction in forest cover in the immediate area. Drier, well drained conditions are further suggested by the presence of *G. pentodon* and *G. procera*. This habitat change probably reflects a response to initial human habitation in the area. The presence of *M. vulgatus*, a synanthropic fauna, is in accord with such a suggestion.

The water table in the nearby channel pond may have been considerably lower given the drop in abundance of aquatic forms. However, the absence of *V. bicarinata* and the low frequency of *C. decisum* may be considered a sampling phenomemon, since specimens of *P. acutum* and *G. parvus* are new introductions into the assemblage.

iii) Level 2

The assemblage from Level 2 contained the highest density of specimens of the four levels at the site (Table 34). However, this sample also reflects the lowest diversity witnessed in the samples (Figure 11). The 23 taxa identified in this assemblage are represented by two dominant, three intermediate, and 18 recedent forms.

The abundance shifts recognized in the preceding level are further emphasized in this level. *P. albilabris* for example, now represents 55.9% of the sample NISP. High artifical calcium introduction into the site through decaying faunal refuse (i.e. bivalves are plentiful) may have acted as an attractant for this calciphile. Marked reductions in abundance of *H. parallelus*, *Z. arboreus*, *H. minuscula*, and several aquatic species suggests an increase in habitat drying and vegetational clearing. *Z. arboreus* for example, is consistently absent in areas devoid of decaying logs. *H. parallelus* on the other hand, is typically a floodplain taxon, rarely found in grassland areas.

The lognormal, but trailing abundance distribution indicates a disturbed or unstable community structure. The most likely cause for this biological response appears to be a perturbation to the environment in the form of cultural activity. Previous records of *P. albilabris* in well-drained pastures, as well as the stable representation of meadow species such as *G. pentodon*, *V. tridentata*, and *G. procera* substantiate the interpretation of vegetational clearing in the area of the site.

iv) Level 1

The assemblage recovered in Level 1 represents a community peculiar to plowed soils. The continued high proportion of P. albilabris indicates that lime rich fertilizers have created an artificial environment for the species. Similarly, the marginal increase in species richness and observed abundance distribution for the sample indicate an unstable community structure that is responding to newly created niche availability.

v) Summary

Quantitative and qualitative data for the Gordon II site gastropod assemblages indicate that at the earliest period of representation, a stable, damp forest gastropod community existed on the site. The area was poorly drained and covered with humus, leaf litter, and hardwood forests. The adjacent channel pond maintained a high water table and supported an abundance of aquatic plants.

The initial human occupation probably began sometime during the accumulation of Level 3 sediments. This occupation prompted a reduction in gastropod community richness. Forest clearing activities favored meadow forms to be attracted to the site.

Furthermore, a number of synanthropic taxa begin to appear in the samples at this time. Increased human activity is postulated for the period represented by the Level 2 sample. This interpretation is most likely given the increased unbalancing in community structure; a trend first observed in the preceding Level 3 sample. Diversity is extremely low for this sample, and most of the fauna indicate that open areas covered in grasses and weeds, as well as artifical calcium concentrations, existed at the site. Unfortunately, the influence of prehistoric and modern agricultural practises on this community cannot be distinguished at this time.

The plow zone assemblage is typically peculiar. Calciphile forms dominate, the abundance distribution is "skewed", and an increase in diversity, all point to the suggestion that periodic non-intensive environmental perturbations in the form of modern agronomic practises are acting on the site.

Hall Shelter site

The Hall Shelter site (15Pe8), Perry County, Kentucky, is located on the east slope of a mountain overlooking the head of Dykes Branch, a small creek which flows into the North Fork of the Kentucky River. The shelter is approximately 3.5 km southeast of Viper, Kentucky (Figure 1).

Details on site location, background research, and analysis of archaeological materials are given by Gatus (1981). Gastropod remains were recovered from an excavation area measuring 2 x 2 meters. Excavation proceeded by arbitrary 10 cm levels with provenience recorded according to four component quadrats (A, B, C, and D) within the excavation area. All sediment was processed in the laboratory using 1.0 mm mesh sieves. Shell remains were then sorted out of the matrix by hand.

A total of 517 specimens representing 25 taxa were recovered from the excavation units. A systematic list of the gastropod taxa identified is given in Table 35. Similarly, the TAXA and NISP data for individual levels for the four excavation units are outlined in Table 36, 37, 38 and 39.

Analysis of archaeological materials by Gatus (1981) indicates several cultural zones are represented at the Hall Shelter. Culturally, Zone I represents the Late Prehistoric and is thought to date to the period A.D. 900 to 1600. Zone II represents a Late Woodland occupation and Zone III represents an Early Woodland occupation. Collectively, the latter two zones cover the period ca. 1000 B.C. to A.D. 900. Zone IVA represents a Late Archaic occupation dating to the period ca. 1700 to 1000 B.C., while Zone IVB represents an Archaic occupation in excess of 3700 B.P.

Viewed individually, level samples are too small to permit interpretation of the changing paleoenvironmental conditions at

Table 35. Systematic list of gastropod taxa identified from the Hall Shelter (15Pe8), Perry County, Kentucky.

Subclass: Prosobranchia
Order: Mesogastropoda

Family: Pleuroceridae
    Goniobasis livescens

Subclass: Pulmonata
Order: Stylommatophora

Family: Polygyridae
    Stenotrema hirsutum
    Stenotrema stenotrema
    Mesodon appressus
    Triodopsis vulgata
    Triodopsis albolabris
    Triodopsis sp.

Family: Zonitidae
    Euconulus fulvus
    Nesovitrea electrina
    Nesovitrea binneyana
    Retinella wheatleyi
    Retinella indentata
    Retinella sculptilis
    Mesomphix sp.
    Paravitrea sp.
    Hawaiia minuscula
    Gastrodonta interna
    Ventridens gularis
    Ventridens demissus
    Ventridens intertextus
    Zonitoides arboreus
    Striatura sp.

Family: Endodontidae
    Anguispira alternata
    Discus patulus
    Helicodiscus parallelus

Table 36. Frequency distribution of gastropod taxa identified in Unit A, by excavation level, from the Hall Shelter site.

	EXCAVATION LEVEL														
TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	SUM
Stenotrema hirsutum		1		1	4	1	3	1	1		1	1	5		19
Mesodon appressus		2							1	1			4	1	9
Triodopsis vulgata												3			3
Triodopsis albolabris		1										1			2
Goniobasis livescens			1							1					2
Retinella wheatleyi													3	1	4
Retinella indentata													1		1
Retinella sculptilis				1											1
Triodopsis sp.													1		1
Mesomphix sp.													1		1
Ventridens gularis				1			1						1		3
Ventridens intertextus					2					1		1	1		5
Anguispira alternata	1	5	3	3	6	4	11	7	3	5	5	7	17	1	78
Discus patulus							4		2			3	4		13
Helicodiscus parallelus													1		1
TOTAL NISP	1	9	4	6	12	5	19	8	7	8	6	16	39	3	143
TOTAL TAXA	1	4	2	4	3	2	4	2	4	4	2	6	11	3	15

Table 37. Frequency distribution of gastropod taxa identified in Unit B, by excavation level, from the Hall Shelter site.

	EXCAVATION LEVEL														
TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	SUM
Stenotrema hirsutum		1			2	4	6	2	3	7	6	5	3		39
Mesodon appressus									1	2	1	1	1		6
Triodopsis albolabris					1						1				2
Goniobasis livescens										1					1
Nesovitrea binneyana													4		4
Retinella wheatleyi													2	1	3
Retinella indentata										1		1			2
Hawaiia minuscula													5	1	6
Ventridens gularis			1					1							2
Ventridens intertextus										1					1
Zonitoides arboreus								1					2		3
Anguispira alternata	1	3		2	7	4	2	8	5	15	7	13	20	4	91
Discus patulus	1	2		2	3	1	4			6	4	5	3		31
Helicodiscus parallelus													3	1	4
TOTAL NISP	2	6	1	4	13	9	12	12	9	33	19	25	43	7	195
TOTAL TAXA	2	3	1	2	4	3	3	4	3	7	5	5	9	4	14

Table 38. Frequency distribution of gastropod taxa identified in Unit C, by excavation level, from the Hall Shelter site.

	EXCAVATION LEVEL														
TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	SUM
Stenotrema hirsutum	1	1	1	6	1	3	1	1				3	1	3	22
Mesodon appressus			1		1	1							1		4
Goniobasis livescens		1													1
Euconulus fulvus														1	1
Nesovitrea electrina													1	3	4
Retinella wheatleyi														1	1
Mesomphix sp.								1	1						2
Hawaiia minuscula														3	3
Ventridens gularis		1	2	3											6
Ventridens demissus		1	1	2											4
Zonitoides arboreus									1	1				2	4
Striatura sp.														1	1
Anguispira alternata		2	3	3	4	2	4		8	2	2	1	5	2	38
Discus patulus						1			4				4		9
Helicodiscus parallelus														2	2
TOTAL NISP	1	6	8	14	6	7	5	2	15	3	2	4	12	18	103
TOTAL TAXA	1	5	5	4	3	4	2	2	5	2	1	2	5	9	16

Table 39. Frequency distribution of gastropod taxa identified in Unit D, by excavation level, from the Hall Shelter site.

	EXCAVATION LEVEL														
TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	SUM
Stenotrema hirsutum	2	2	1	3	6		4		1				4		23
Stenotrema stenotrema	1														1
Mesodon appressus									1				1		2
Goniobasis livescens	1		1												2
Nesovitrea electrina													1		1
Nesovitrea binneyana													1		1
Paravitrea sp.		1													1
Hawaiia minuscula													4	6	10
Gastrodonta interna			1												1
Ventridens gularis			3												3
Anguispira alternata	3	3	4	9	16		18		1	1		3	10	1	69
Discus patulus			1	1	5		1		1			1	1	1	12
Helicodiscus parallelus												1	2		3
TOTAL NISP	7	7	11	13	27	0	23	0	4	1	0	5	24	8	130
TOTAL TAXA	4	3	6	3	3	0	3	0	4	1	0	3	8	3	13

the site. As is evident in Table 40, NISP values are very low, ranging from five to 94. Data from the individual excavation units were therefore grouped for further analysis. Table 41 provides the grouped frequency distributions for gastropods by excavation level, while Table 42 provides frequency distributions by cultural zones. The result of this frequency grouping is an increase in the observed NISP range to a low of 39 and a high of 231. These quantitative data, as well as the assembled ecological information for specific taxa (Appendix V) provide a basis for evaluating the shifting paleoenvironmental conditions at the Hall Shelter.

i) Zone IVB

The earliest time period represented at the site consists of the Zone IVB sediments. The gastropod sample from this zone is very high in species richness (Figure 10) and is thought to reflect a stable rock shelter community. Of the taxa recovered, four are dominant, three intermediate, and 11 are recedent.

With respect to the dominant species, both A. alternata and H. patulus are open woodland forms that favor damp conditions. S. hirsutum is also a moist habitat snail that prefers steep hillsides, oak ridges and southern exposures. Vegetatively, both H. patulus and S. hirsutum are commonly found associated with beech-yellow birch stands.

Table 40. Summary frequency distributions of taxa identified in the individual units, by cultural zones, from the Hall Shelter site.

		CULTURAL ZONES					
UNIT		I	II	III	IVA	IVB	SUM
A	NISP	10	10	17	42	61	143
	TAXA	4	5	3	7	13	15
B	NISP	8	5	22	66	94	195
	TAXA	3	3	4	9	11	14
C	NISP	7	22	13	25	36	103
	TAXA	5	5	4	5	11	16
D	NISP	14	24	27	28	37	130
	TAXA	5	6	3	4	8	13
	TOTAL NISP	39	61	79	161	231	571
	TOTAL TAXA	10	9	6	10	19	25

Table 41. Frequency distribution of gastropod taxa identified in total sample (Units A, B, C and D), by excavation level, from the Hall Shelter site.

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	SUM
	EXCAVATION LEVEL														
Stenotrema hirsutum	3	5	2	10	13	8	14	4	5	7	7	9	13	3	103
Stenotrema stenotrema	1														1
Mesodon appressus		2	1		1	1			3	3	1	1	7	1	21
Triodopsis vulgata												3			3
Triodopsis albolabris		1			1						1	1			4
Goniobasis livescens	1	1	2							2					6
Euconulus fulvus														1	1
Nesovitrea electrina													2	3	5
Nesovitrea binneyana													5		5
Retinella wheatleyi													5	3	8
Retinella indentata									1	1		1	1		4
Retinella sculptilis				1											1
Triodopsis sp.													1		1
Mesomphix sp.								1	1				1		3
Paravitrea sp.		1													1
Hawaiia minuscula													9	10	19
Gastrodonta interna			1												1
Ventridens gularis		1	6	4			1	1					1		14
Ventridens demissus		2	1	2											5
Ventridens intertextus					2					2		1	1		6
Zonitoides arboreus								1	1	1			2	2	7
Striatura sp.														1	1

Table 41 (continued)

Anguispira alternata	5	13	10	17	33	10	35	15	17	23	14	24	52	8	276
Discus patulus	1	2	1	3	8	2	9		7	6	4	9	12	1	65
Helicodiscus parallelus												1	6	3	10
TOTAL NISP	11	28	24	37	58	21	59	22	35	45	27	50	118	36	571
TOTAL TAXA	5	9	8	6	6	4	4	5	7	8	5	9	15	11	25

Table 42. Frequency distribution of gastropod taxa identified in total sample (Units A, B, C and D), by cultural zones, from the Hall Shelter site.

TAXA	CULTURAL ZONES I	II	III	IVA	IVB	SUM
Stenotrema hirsutum	8	12	21	30	32	103
Stenotrema stenotrema	1					1
Mesodon appressus	2	1	2	6	10	21
Triodopsis vulgata					3	3
Triodopsis albolabris	1		1		2	4
Goniobasis livescens	2	2		2		6
Euconulus fulvus					1	1
Nesovitrea electrina					5	5
Nesovitrea binneyana					5	5
Retinella wheatleyi					8	8
Retinella indentata				2	2	4
Retinella sculptilis		1				1
Triodopsis sp.					1	1
Mesomphix sp.				2	1	3
Paravitrea sp.	1					1
Hawaiia minuscula					19	19
Gastrodonta interna		1				1
Ventridens gularis	1	10		2	1	14
Ventridens demissus	2	3				5
Ventridens intertextus			2	2	2	6
Zonitoides arboreus				3	4	7
Striatura sp.					1	1
Anguispira alternata	18	27	43	90	98	276
Discus patulus	3	4	10	22	26	65
Helicodiscus parallelus					10	10
TOTAL NISP	39	61	79	161	231	571
TOTAL TAXA	10	9	6	10	19	25

Intermediate species such as *M. appressus*, prefer calcareous soils, hardwood forests underlain with rocky rubble, gravel hills and foothill regions, while *P. wheatleyi* is known to favor humid slopes and oak woods. *H. minuscula* and *H. parallelus* are two other forms that favor decaying wood, shade, and damp situations.

Recedent species include *T. albolabris*, a species known to occur on bushy slopes, limestone terrain and in beech-maple stands, as well as *N. electrina*, a hydrophilic gastropod, rarely observed in open areas or in areas with an annual rainfall not exceeding 35 inches. Another recedent form identified in this sample is *R. indentata*. This snail is known to occur in quarries and woodlands of oak, elm and maple. Bluff and forested slope species identified in the sample include *V. gularis* and *V. intertextus*. The latter species is commonly found in association with the dominant *A. alternata*.

In general, all of the species identified in Zone IVB represent that type of community structure which may be expected to occur in rock shelters (Hubricht 1964b). The majority of forms favor well-shaded, damp areas or bushy slopes and high bluffs. Additionally, several species typically prefer rocky, limestone terrains. Unfortunately, strict troglobitic species (Jefferson 1976) such as *Carychium stygium* (Hubricht 1960) or the blind cave snail *Amnicola cora* (Hubricht 1979) were not found in the sample.

ii) Zone IVA

The gastropod assemblage from this zone shows a slight reduction in species richness (Figure 10). Of the 10 species identified, three are dominant, one is intermediate, and six are recedent. In terms of abundance, the three dominant taxa all show slight increases in their proportional representation relative to Zone IVB (Table 43). Furthermore, the disproportionate character of the assemblage suggests some form of perturbation may have been acting on the previously stable community. Environmentally, conditions were probably similar to those postulated in Zone IVB.

Noteworthy, is the presence of the the freshwater snail *G. livescens*; an unquestionable introduction by the shelter's inhabitants. Gatus' (1981) interpretation of the archaeological record suggests that human occupation in the shelter, during this period was both intermittent and non-intensive. This interpretation appears sound given the marginal reduction in gastropod diversity from the preceding level and the total elimination of several sensitive species such as *N. electrina*, *H. parallelus*, and *N. binneyana*.

iii) Zone III

As illustrated in Figure 10, the gastropod sample from this zone shows the greatest reduction in species richness observed in the Hall Shelter samples. Of the taxa identified, half are

Table 43. Proportional distribution of gastropod taxa identified in total sample (Units A, B, C and D), by cultural zones, from the Hall Shelter site.

TAXA	CULTURAL ZONES I	II	III	IVA	IVB	SUM
Stenotrema hirsutum	.205	.197	.266	.186	.138	.180
Stenotrema stenotrema	.026					.002
Mesodon appressus	.051	.016	.025	.037	.043	.037
Triodopsis vulgata					.013	.005
Triodopsis albolabris	.026		.013		.009	.007
Goniobasis livescens	.051	.033		.012		.010
Euconulus fulvus					.004	.002
Nesovitrea electrina					.022	.009
Nesovitrea binneyana					.022	.009
Retinella wheatleyi					.035	.014
Retinella indentata				.012	.009	.007
Retinella sculptilis		.016				.002
Triodopsis sp.					.004	.002
Mesomphix sp.				.012	.004	.005
Paravitrea sp.	.026					.002
Hawaiia minuscula					.082	.033
Gastrodonta interna		.016				.002
Ventridens gularis	.026	.164		.012	.004	.024
Ventridens demissus	.051	.049				.009
Ventridens intertextus			.025	.012	.009	.010
Zonitoides arboreus				.019	.017	.012
Striatura sp.					.004	.002
Anguispira alternata	.462	.447	.544	.559	.424	.483
Discus patulus	.077	.066	.126	.137	.113	.114
Helicodiscus parallelus					.043	.018
TOTAL NISP	39	61	79	161	231	571
TOTAL TAXA	10	9	6	10	19	25

dominant, and these represent 93.6% of the total NISP. Similarly, the abundance distribution for the assemblage typifies that form of distribution known to occur in highly disturbed or polluted environments (May 1976).

In this particular case, the environmental perturbation assumed to have prompted the successional drop in diversity, is increased human occupation. The natural environment appears to have remained stable relative to preceding conditions. On the other hand, the archaeological record as interpreted by Gatus (1981) suggests this zone represents the most intensive period of occupation in the shelter's history. Note for example, that an increase in proportional abundance of _T. albolabris_ in the sample may be expected in a culturally disturbed situation, since this taxon is a known synanthropic snail. The dominant fauna remains primarily ubiquitous; pioneering taxa dominating the disturbed habitat.

iv) Zone II

The gastropod assemblage from Zone II indicates both autogenic and allogenic succession. Several integrating taxa such as _R. sculptilis_ appear in the sample and a number of pioneering forms such as _A. alternata_ show a reduction in abundance.

In many ways, the reorganization in community structure fulfills theoretical expectations of a biological community response to an earlier cultural perturbation. For example, the appearance of G. interna into the assemblage indicates this particular species' preference to fire. Furthermore, the sudden increase in abundance of V. demissus is expected, since this species is a typical synanthropic form. These observations, in combination with an increase in species richness characterize the allogenic aspect of the successional shift.

The autogenic aspect of succession is represented by ranked abundance changes in the species. For example, V. gularis assumes a more prominent position in the abundance hierarchy. This observation may be expected as this species is a common snail in shelters and on bluff regions. Several other taxa, such as S. hirsutum and H. patulus show a reduction in their proportional abundance; a response expected to represent a prestabilization of an earlier pioneering peak.

Human occupation in the shelter was less intense at this time than that postulated during Zone III. Both the gastropod record and the archaeological record (Gatus 1981) support this conclusion. One inexplicable, but interesting observation is the proportional abundance increase of the freshwater snail G. livescens. This change is difficult to interpret, but may indicate a greater emphasis on riverine resource exploitation. However, this change may in fact reflect an unknown sampling phenomenon.

v) Zone I

The final sample from the Hall Shelter represents both Late Prehistoric occupation and modern accumulations. The archaeological evidence suggests that only periodic occupation occurred at the shelter at this time (Gatus 1981). The gradual increase in species richness is consistent with the archaeological interpretation (Figure 10).

Of the 10 species identified in this sample, three are dominant, three intermediate, and four are recedent. This successional change in the deposit is primarily autogenic, that is, interspecific behavioral control independent of environmental stimuli. Autogenic importance is most likely, since several taxa such as *A. alternata*, *D. patulus*, and *S. hirsutum* remain relatively stable in their proportional abundance, while integrating species such as *S. stenotrema* and *Paravitrea* sp. begin to show only marginal representation. In other words, the microenvironment in the shelter began to stabilize in the absence of cultural disturbance. Such a stabilization would permit environmentally neighboring species such as *S. stenotrema*, a forested slope snail, and *Paravitrea* sp., a high bluff fauna, to enter the shelter gastropod community.

vii) Summary

Most of the gastropods identified in samples from the Hall Shelter typify rock shelter microenvironments. The natural environment in the area of the shelter appears to have remained stable during the known occupational history of the site. Basically, taxa identified indicate a high altitude situation, one that provided shade and moisture for the resident molluscs.

Modification to the gastropod communities was probably the result of human occupation in the shelter. The sample from Zone IVA suggests a non-intensive periodic occupation occurred during the period encompassed by the sediments. A significant reduction in species richness for the Zone III assemblage correlates well with the archaeologically assumed increase in human occupation (Gatus 1981). This drop in gastropod diversity was initially apparent in the Zone IVA sample. The subsequent assemblage from Zone II substantiates the above postulate for intensive human occupation during Zone III, as well as a marked reduction in occupation during Zone II. Interpretation of the Zone I sample suggests a gradual return to a natural gastropod rock shelter community following a further decrease in human activity at the locus.

Summary

The purpose of this chapter was to illustrate the methodology of paleoenvironmental interpretations employing nonmarine gastropods as a data base. Several different case studies were presented representing a variety of environmental habitats to indicate possible inter-locational variation.

Additionally, where applicable, simple statistical analyses were employed to illustrate the misconception characterizing current quantophobic approaches to molluscan zooarchaeology. Finally, I attempted to illustrate how quantitative analyses in the form of diversity measurements may be used in conjunction with classical qualitative approaches to augment the methodology of paleoenvironmental analysis.

6. Conclusion

This study presents the results of an analysis of gastropod samples from a number of archaeological deposits. The primary objective was to provide an interpretation of changing cultural and natural environmental conditions at the localities on the basis of recovered gastropod shells. Additionally, I attempted to introduce several new quantitative approaches to the existing methodological repertoire of paleoecological analysis.

Early studies in molluscan zooarchaeology viewed gastropod remains from archaeological sites as sources for inferring paleoclimatic conditions, useful chronostratigraphic markers and evidence of prehistoric dietary patterns. These theoretical and methodological developments during the first 100 years of research were extremely useful in structuring current approaches to archaeological gastropod analysis.

Our present day understanding of shell remains from archaeological sites reflects a philosophy based on a taphonomic framework. As indicated in this study, a researcher must assess all the potential means for shell introduction into sites, evaluate the sample under examination with respect to these mechanisms, and then proceed with an interpretation of the remains. Assuming a natural or accidental introduction, a researcher can then attempt a paleoecological interpretation of the past conditions characterizing the cultural loci.

This interpretation of paleoecology should exceed simple qualitative analysis. Hence, this study attempted to emphasize a quantitative methodology to analysis. In attaining this goal, I reviewed a number of aspects directly associated with quantitative interpretations. A review of numerical data presentation in the published record indicated a lack of pertinent information and an absence of consistency among reports. Those few studies which do provide essential numerical information were then relied upon to generate a model for quantifying diversity. Arguments were presented to illustrate the validity and applicability of the new diversity measurement for gastropod analysis.

The measurement of species richness and its relationship to environmental parameters was examined and shown to be amenable to refining paleoecological interpretations. This association was later applied to several case studies to illustrate how changing prehistoric conditions could be recognized through gastropod analysis.

Additional quantitative emphasis was placed on the biases inherent in poor and variable collection strategies. One example of a sieving experiment was presented to illustrate the variability resulting from poor collection. Similarly, sampling for gastropods was shown to be a function of sample size, when sample size is viewed in terms of number of identifiable specimens. This approach proved useful for further attempts at assessing the statistical adequacy of individual samples in regard to the proportional abundances of specific taxa. Finally, application of the truncated lognormal distribution to snail assemblages was shown to be a successful method for determining what percentage of species in a population occur in the sample.

Modern ecological data were collected for the taxa identified in this study and included as an appendix to the thesis. This information was synthesized in the qualitative interpretations of various assemblages. Further, the quantitative reasonings developed in chapters three and four were integrated into the final interpretations of site samples to further the potential contributions of gastropod remains to archaeology. As indicated in the various case studies, both cultural and natural environmental patterns could be discerned in such an approach.

In the end, this study attempted to view gastropod remains as potential information sources to archaeology. Quantitative and qualitative approaches were integrated in assessing several archaeological gastropod samples. Hopefully, the results of this study will prove to be of use in future archaeological endeavors.

Appendix I: Raw NISP and TAXA data for freshwater, terrestrial and non-marine gastropods from various published sources.

Reference	MESOGASTROPODA/ BASOMMATOPHORA		STYLOMMATOPHORA		PROSCERANCHIA/ PULMONATA	
	NISP	TAXA	NISP	TAXA	NISP	TAXA
Sparks 1962	4	3	-	-	4	3
	363	4	-	-	363	4
	842	6	-	-	842	6
	806	4	-	-	806	4
	737	5	-	-	737	5
	925	7	-	-	925	7
	704	5	-	-	704	5
	465	4	-	-	465	4
	526	5	-	-	526	5
	358	5	-	-	358	5
	305	4	-	-	305	4
	411	3	-	-	411	3
	609	4	-	-	609	4
	793	5	-	-	793	5
	891	5	1	1	892	6
	589	5	-	-	589	5
Sparks 1954	17	5	16	3	33	8
	6	2	126	4	132	6
	-	-	25	2	25	2
	2	1	34	1	36	2
	25	7	503	21	528	30
	6	3	317	30	323	33
	13	5	1577	33	1590	38
Turner 1970	-	-	5	4	5	4
Burchell 1965	-	-	11	3	11	3
	-	-	193	7	193	7
	1	1	2472	7	2473	8
	-	-	218	5	218	5
	-	-	230	6	230	6
	-	-	116	12	116	12
	-	-	48	9	48	9
	-	-	23	5	23	5
	-	-	134	6	134	6
	-	-	392	13	392	13
	-	-	120	12	120	12
Sparks 1957-58	9	1	1	1	10	2
	40	3	4	4	44	7
	32	5	1	1	33	6

	243	7	-	-	243	7
	390	7	-	-	390	7
	656	9	5	3	661	12
	2768	9	6	6	2774	15
	395	10	1	1	396	11
	1148	13	8	5	1156	18
	2230	13	6	5	2236	18
	1937	11	4	3	1941	14
	2001	11	1	1	2002	12
	5050	14	85	10	5135	24
	3172	17	111	9	3283	28
	3122	16	102	10	3224	26
	2330	16	319	16	2649	32
	2733	16	500	24	3233	40
	2471	15	546	22	3017	37
	1075	16	178	16	1253	32
	555	14	82	13	637	27
	348	16	60	15	408	31
	325	13	66	13	391	26
	97	7	115	14	212	21
Miller 1968	937	16	925	19	1862	35
	592	11	2055	19	2647	30
Miller 1970	5692	22	8645	27	14337	49
Burchell and Davis 1957	15	3	426	10	441	13
	8	2	621	11	629	13
	4	2	191	11	195	11
	10	2	373	10	383	12
	12	4	180	19	192	23
	7	2	171	18	176	20
	16	3	424	21	440	24
	5	2	160	20	165	22
	2	1	129	20	131	21
	1	1	162	16	163	17
	-	-	157	21	157	21
	4	1	798	36	802	37
	8	3	253	24	261	27
	186	7	404	21	590	28
West et. al. 1974	19	6	6	2	25	8
	1476	10	83	8	1559	18
	4	3	1	1	5	4
	793	11	4061	11	4854	22
	558	18	1741	9	2299	27
	115	10	396	7	511	17
	3	2	6	5	9	7
	6	5	266	3	272	8
	6	4	133	3	139	7

	12	6	274	3	286	9
	143	12	860	6	1003	18
	164	14	1670	7	1834	21
	60	7	251	3	311	10
	7	4	74	2	81	6
Sparks and West 1964	11	4	3	3	14	7
	1	1	4	3	5	4
	7	4	6	6	13	10
	5	3	11	9	16	12
	25	6	40	17	65	23
	67	10	46	12	113	22
	31	6	34	12	65	18
	6	3	16	12	22	15
	16	5	22	13	38	18
	187	16	269	29	456	45
	62	14	147	25	209	39
	121	16	137	25	258	41
	100	15	105	19	205	34
	20	9	26	12	46	21
	41	11	100	19	141	30
	169	16	222	26	391	42
	81	13	134	20	215	33
	65	13	13	5	78	18
	397	18	55	11	452	29
	280	15	36	11	316	26
	581	14	47	8	628	32
	106	7	2	2	108	9
	58	6	1	1	59	7
Getz and Hibbard 1965	-	-	-	-	57246	38
	-	-	-	-	1083	19
	-	-	-	-	2533	25
Kerney 1957a	95	7	252	22	347	29
	243	7	140	16	383	23
	87	9	231	21	318	30
	36	5	101	19	137	24
Kerney 1957b	-	-	2584	34	2584	34
Tuthill 1963a	246	5	3	2	249	7
Karrow, Clarke and Herrington 1972	5	2	-	-	5	2
	19	3	-	-	19	3
	36	4	68	6	104	10
	42	5	-	-	42	5
	43	3	-	-	43	3
	2	1	3	1	5	2
	536	6	15	2	551	8

Zoltai 1969	9	2	-	-	9	2
	39	5	-	-	39	5
	54	8	-	-	54	8
	12	2	-	-	12	2
	51	7	-	-	51	7
	506	4	-	-	506	4
Davis and Pitchford 1958	186	11	456	26	642	37
	56	2	47	6	103	8
	68	6	168	15	236	21
	3844	12	4538	34	8382	46
Sparks and West 1968	919	6	-	-	919	6
	17	6	-	-	17	6
	1560	13	3	2	1563	15
	531	7	-	-	531	7
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Piechocki 1977	285	4	9081	12	9366	16
	3	2	61	8	64	10
	4	2	63	8	67	10
	53	1	333	14	386	15
	69	2	90	12	159	14
	9	2	231	18	240	20
	98	6	3632	32	3730	38
	121	5	4268	35	4389	40
	70	4	7850	43	7920	47
	449	4	4886	36	5335	40
	297	4	7716	48	8013	52
	196	4	11317	54	11513	58
	228	3	8520	53	8748	56
	148	3	4633	48	4781	51
	24	3	5750	49	5774	52
	155	5	6305	53	6460	58
	249	4	5103	48	5352	52
	19	3	1553	44	1572	47
	8	3	350	32	358	35
	37	3	364	29	401	32
	-	-	10	6	10	6
	1	1	45	12	46	13
	1	1	50	15	51	16
	3	1	25	13	28	14
	1	1	1851	45	1852	46
Kerney, Brown and Chandler 1964	3	1	-	-	3	1
	2	1	-	-	2	1
	11	2	30	4	41	6
	10	1	53	6	63	7
	5	1	18	4	23	5
	5	1	93	9	98	10

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37	1	758	13	795	14
56	2	2161	17	2217	19
342	2	83	9	425	11
168	2	75	8	243	10
27	2	45	7	72	9
31	2	46	11	77	13
13	2	42	8	55	10
16	2	56	15	72	17
14	3	59	17	73	20
76	2	234	16	310	18
7	1	83	14	90	15
-	-	5	3	5	3
48	1	131	6	179	7
489	2	1111	16	1600	18
198	1	521	14	719	15
21	2	20	9	41	11
15	2	23	10	38	12
44	2	168	16	212	18
5	2	31	10	36	12
9	2	53	12	62	14
1	1	27	10	28	11
-	-	96	15	96	15
4	1	59	12	63	13
-	-	40	12	40	12
1	1	91	14	92	15
7	1	118	17	125	18
3	1	67	15	70	16
6	1	137	16	143	17
4	1	31	10	35	11
5	1	74	13	79	14
-	-	5	5	5	5
38	2	112	12	150	14
18	1	68	12	84	13
33	1	270	18	303	19
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1	1	20	7	21	8
8	1	213	19	221	20
53	1	352	10	405	11
15	1	44	5	59	6
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14	1	42	11	66	12
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-	-	89	12	89	12
4	1	45	11	49	12
20	1	87	10	107	11

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3848	4	4103	15	7951	19
56	4	324	13	380	17
37	2	155	13	192	15
272	3	1053	17	1325	20
140	4	1250	18	1390	22
68	2	509	17	577	19
48	2	201	16	249	18
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-	-	293	21	293	21
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-	-	313	24	313	24
-	-	291	24	291	24
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-	-	1041	30	1041	30
-	-	21	8	21	8
-	-	21	9	21	9
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-	-	515	28	515	28
-	-	748	30	748	30
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1	1	519	30	520	31
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	-	-	854	34	854	34
	-	-	21	7	21	7
	-	-	30	9	30	9
	-	-	73	7	73	7
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	-	-	57	10	57	10
	-	-	135	16	135	16
	2	1	531	26	533	27
	10	1	926	28	936	29
	10	1	1225	29	1235	30
	12	1	963	28	975	29
	14	1	944	27	958	28
	25	1	388	24	413	25
	11	1	940	26	951	27
	10	1	599	26	609	27
	13	1	1124	27	1137	28
	6	1	1005	27	1011	28
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Kerney 1963	-	-	3	1	3	1
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	-	-	5	3	5	3
	-	-	18	4	18	4
	-	-	71	4	71	4
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	-	-	221	10	221	10
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	-	-	97	7	97	7
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-	-	668	15	668	15
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-	-	202	10	202	10
-	-	191	10	191	10
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-	-	125	10	125	10
-	-	156	13	156	13
-	-	120	10	120	10
-	-	163	12	163	12
-	-	162	13	162	13
-	-	384	12	384	12
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-	-	182	4	182	4
-	-	367	8	367	8
-	-	22	4	22	4
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-	-	942	14	942	14
-	-	858	13	858	13
-	-	1059	13	1059	13
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-	-	80	10	80	10
-	-	105	10	105	10
-	-	64	11	64	11
-	-	135	13	135	13
-	-	199	11	199	11
-	-	116	11	116	11
-	-	163	13	163	13
-	-	208	13	208	13
-	-	151	13	151	13
-	-	141	13	141	13
-	-	116	13	116	13
-	-	68	10	68	10
-	-	46	9	46	9
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-	-	130	18	130	18
-	-	166	21	166	21
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-	-	91	7	91	7
-	-	107	7	107	7
-	-	360	6	360	6
-	-	628	6	628	6
-	-	163	5	163	5
-	-	181	7	181	7
-	-	411	6	411	6
-	-	399	11	399	11
-	-	419	9	419	9
-	-	474	11	474	11
-	-	613	12	613	12
-	-	605	11	605	11
-	-	735	14	735	14
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-	-	681	14	681	14
-	-	194	14	194	14
-	-	202	14	202	14
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-	-	181	13	181	13
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-	-	96	11	96	11
-	-	76	11	76	11
-	-	74	8	74	8
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Sparks and West 1970	30	4	13	5	43	9
	45	4	14	8	59	12
	698	19	243	21	941	40
	1291	19	260	31	1551	50
	314	15	46	10	360	25
	267	15	130	25	397	40
	599	14	333	31	932	45
	493	14	416	31	909	45
	232	14	111	28	343	42
	2311	17	771	32	3082	49
	130	6	44	14	174	20
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	2	2	-	-	2	2
	71	5	3	3	74	8
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	1	1	1	1	2	2
	189	9	13	6	202	15
	875	14	78	13	953	27
	647	12	51	13	698	25
	1046	17	151	12	1197	29
	831	18	111	9	942	27
	564	16	10	3	574	19
	1063	13	2	2	1065	15
	2595	17	6	4	2601	21
	489	13	6	4	495	17
	144	9	8	3	152	12
	42	8	42	13	84	21
	621	14	81	15	702	29
	2996	18	184	21	3180	39
	2654	15	233	21	2887	36
	1	1	-	-	1	1
	122	13	127	18	249	31
	2	1	-	-	2	1
	15	6	2	1	17	7
	10	5	-	-	10	5
	2142	15	12	5	2154	20
	5106	19	42	9	5148	28
	19	6	6	2	25	8
	1476	10	83	8	1559	18
	4	3	1	1	5	4
	2	1	7	4	9	5
	19	3	2	2	21	5
	346	10	38	12	384	22
	433	9	21	6	454	15
	276	10	16	10	292	20
	119	7	6	3	125	10
	191	8	39	12	230	20
	31	6	10	5	41	11
	28	4	8	4	36	8

	102	7	26	8	128	15
	15	2	9	6	24	8
	19	1	14	4	33	5
	145	10	11	9	156	19
	134	10	4	4	138	14
	91	7	4	3	95	10
	54	5	2	2	56	7
	55	7	-	-	55	7
	189	11	2	1	191	12
	192	10	1	1	193	11
	806	13	96	15	902	28
Stratton 1970b	-	-	376	6	376	6
	-	-	781	9	781	9
	-	-	310	7	310	7
Sparks and Grove 1961	992	6	46	4	1038	10
	555	7	7	2	562	9
	1053	8	5	2	1058	10
	86	8	39	5	125	13
Dimbleby and Evans 1974	-	-	108	16	108	16
Wilson and La Rocque 1973	3	2	11	3	14	5
Cooper 1972	23	7	1	1	24	8
	3	1	-	-	3	1
	240	7	52	4	292	11
	144	18	7	4	151	22
	15	4	1	1	16	5
	12	3	-	-	12	3
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	60	11	-	-	60	11
	31	10	3	3	34	13
	13	4	4	1	17	5
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Evans and Valentine 1974	-	-	151	24	151	24
	-	-	13	7	13	7
	-	-	5	3	5	3
	-	-	148	19	148	19
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Altena and Kuiper 1945	9	4	3	1	12	5
	46	7	1	1	47	8
	129	11	1	1	130	12
	281	13	3	1	284	14
	19	2	-	-	19	2
	45	4	2	2	47	6
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Turk 1966	-	-	4	2	4	2
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	-	-	33	13	33	13
	-	-	180	20	180	20
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	-	-	142	8	142	8
Wayne 1959	2	1	589	19	591	20
	4	2	185	8	189	10
	125	1	236	17	361	18
	-	-	66	4	66	4
	65	1	240	9	305	10
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	91	1	681	19	772	20
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	-	-	480	9	480	9
	68	1	399	11	467	12
	10	1	208	10	218	11
	-	-	225	6	225	6
	418	1	181	2	599	3
	35	1	71	8	106	9
van der Schalie 1953	969	15	2301	28	3267	43
Hibbard and Taylor 1960	134397	20	3502	24	137899	44
Reynolds 1959	305	7	-	-	305	7
	5663	8	-	-	5663	8
	8044	11	-	-	8044	11
Aukeman 1960	17350	15	-	-	17350	15
	12894	16	-	-	12894	16
Cornejo 1961	972	7	-	-	972	7
	924	8	-	-	924	8
	9780	11	-	-	9780	11
	1535	10	-	-	1535	10
	371	7	-	-	371	7
	670	8	-	-	670	8
La Rocque and Forsyth 1957	8	1	230	10	238	11
	-	-	286	11	286	11
Zimmerman 1960	18932	14	-	-	18932	14
	875	11	-	-	875	11
	851	10	1	1	851	11

Mowery 1961	5363	11	117	3	5480	14
	898	11	99	3	997	14
	12672	13	528	3	13200	16
	1901	13	524	5	2425	18
Sheatsley 1960	480	2	122	3	602	5
	2027	7	235	3	2262	10
	3010	10	61	4	3071	14
	159	7	6	2	165	9
Clark 1961	3372	8	2435	16	5807	24
	2250	8	1556	15	3806	23
	12599	9	4269	16	16868	25
	442	8	1416	14	1858	22
van der Schalie 1940	-	-	51	9	51	9
van der Schalie 1939	1	1	115	17	116	18
Dennis 1928	63	7	-	-	63	7
	90	8	5	1	95	9
	21	5	-	-	21	5
	20	4	-	-	20	4
Hubricht 1964c	-	-	247	21	247	21
	-	-	1153	27	1153	27
	-	-	196	26	196	26
	-	-	28	8	28	8
	-	-	78	16	78	16
	-	-	25	5	25	5
	-	-	1065	29	1065	29
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	151	8	104	18	255	26
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	-	-	2029	46	2029	46
	-	-	201	15	201	15
	-	-	2181	44	2181	44
	-	-	520	32	520	32
	-	-	531	32	521	32
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Kerney 1976a	1	1	346	31	347	32
	174	4	2360	33	2534	37
Cameron 1978b	-	-	531	5	531	5
	-	-	100	4	100	4
	-	-	27	5	27	5

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	-	-	26	5	26	5
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	-	-	42	5	42	5
	-	-	26	2	26	2
	-	-	31	4	31	4
	-	-	54	6	54	6
	-	-	31	2	31	2
Jaeckel 1950	-	-	722	34	722	34
	-	-	423	26	423	26
	-	-	60	13	60	13
	-	-	53	18	53	18
	-	-	728	32	728	32
	-	-	4667	38	4667	38
	-	-	53	17	53	17
	-	-	22659	53	22659	53
	-	-	73	29	73	29
Baerreis 1974	1	1	804	15	805	16
	-	-	53	9	53	9
	2	2	1794	19	1796	21
	1	1	33	9	34	10
	2	1	217	14	219	15
Sparks and Lambert 1961	128	4	117	13	245	17
	33	3	18	8	51	11
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632	14	-	-	632	14
674	14	1	1	675	15
699	13	-	-	699	13
663	13	1	1	664	14
784	15	1	1	785	16
733	13	1	1	734	14
545	12	-	-	545	12
798	12	-	-	798	12

711	14	-	-	711	14
902	12	-	-	902	12
680	12	-	-	680	12
700	12	-	-	700	12
517	10	-	-	517	10
543	9	-	-	543	9
664	10	-	-	664	10
891	11	-	-	891	11
776	8	-	-	776	8
299	8	-	-	299	8
178	7	-	-	178	7
683	9	-	-	683	9
407	9	-	-	407	9
262	7	-	-	262	7
189	6	-	-	189	6
63	5	-	-	63	5
204	6	-	-	204	6
31	7	-	-	31	7
41	6	-	-	41	6
31	4	-	-	31	4
33	6	-	-	33	6

Appendix II: References from which raw data on TAXA and NISP was collected in generating descriptive equations 1 to 24. (Q = Quaternary, I = Interglacial, G = Glacial and H = Holocene)

FRESHWATER

SOURCE	ENGLAND				NORTH AMERICA			UNIVERSAL
	Q	I	G	H	Q	G	H	Q
Sparks 1962	x							x
Sparks 1954	x							x
Burchell 1965	x							x
Sparks 1957-58	x	x						x
Miller 1976					x	x		x
Miller 1970					x	x		x
Burchell & Davis 1957	x							x
West et al. 1974	x		x					x
Sparks & West 1964	x	x						x
Kerney 1957a								x
Tuthill 1963					x	x		x
Karrow et al. 1972					x			x
Zoltai 1969					x		x	x
Davis & Pitchford 1958	x			x				x
Sparks & West 1968	x	x						x
Piechocki 1977								x
Kerney et al. 1964	x			x				x
Sparks & West 1970	x	x						x
Sparks & Grove 1961								x
Wilson & La Rocque 1973					x		x	x
Cooper 1972	x	x						x
Altena & Kuiper 1945								x
Wayne 1959a					x	x		x
Wayne 1959b					x		x	x
van der Schalie 1953					x			x
Hibbard & Taylor 1960					x			x
Reynolds 1959					x	x		x
Aukeman 1960					x	x		x
Cornejo 1961					x	x		x
La Rocque & Forsyth 1957					x	x		x
Zimmerman 1960					x	x		x
Mowery 1961					x	x		x
Sheatsley 1960					x	x		x
Clark 1961					x	x		x
van der Schalie 1939					x		x	x
Dennis 1928					x		x	x
Hubricht 1964c					x			x
Kerney 1976a	x			x				x

Baerreis 1974					x		x	x
Sparks & Lambert 1961	x			x				x
Evans 1966	x							x
Clark 1962					x		x	x
Luttig 1953								x
Devore 1975					x	x		x
Evans 1972	x			x				x
Olle 1969					x	x		x
Bickel 1970					x	x		x

TERRESTRIAL

SOURCE	ENGLAND				NORTH AMERICA			UNIVERSAL
	Q	I	G	H	Q	G	H	Q
Sparks 1962	x							x
Sparks 1954	x							x
Turner 1970	x							x
Burchell 1965	x							x
Sparks 1957-58	x	x						x
Miller 1976					x	x		x
Miller 1970					x	x		x
Burchell & Davis 1957	x							x
West et al. 1974	x		x					x
Sparks & West 1964	x	x						x
Kerney 1957a								x
Kerney 1957b	x			x				x
Tuthill 1963					x	x		x
Karrow et al. 1972					x			x
Davis & Pitchford 1958	x			x				x
Sparks & West 1968	x	x						x
Piechocki 1977								x
Kerney et al. 1964	x			x				x
Kerney 1963	x		x					x
Sparks & West 1970	x	x						x
Stratton 1970b	x			x				x
Sparks & Grove 1961								x
Dimbleby & Evans 1974	x			x				x
Wilson & La Rocque 1973					x		x	x
Cooper 1972	x	x						x
Evans & Valentine 1974	x			x				x
Altena & Kuiper 1945								x
Turk 1966	x			x				x
Wayne 1959a					x	x		x
Wayne 1959b					x		x	x
van der Schalie 1953					x			x
Hibbard & Taylor 1960					x			x
La Rocque & Forsyth 1957					x	x		x

Zimmerman 1960					x	x		x
Mowery 1961					x	x		x
Sheatsley 1960					x	x		x
Clark 1961					x	x		x
van der Schalie 1940					x		x	x
van der Schalie 1939					x		x	x
Dennis 1928					x		x	x
Hubricht 1964c					x			x
Kerney 1976a	x			x				x
Cameron 1978b	x			x				x
Jaeckel 1950								x
Baerreis 1974					x		x	x
Sparks & Lambert 1961	x			x				x
Evans 1966	x							x
Clark 1962					x		x	x
Luttig 1953								x
Pauken 1969					x	x		x
Devore 1975					x	x		x
Evans 1972	x			x				x
Olle 1969					x	x		x
Bickel 1970					x	x		x

MIXED FRESHWATER/TERRESTRIAL

SOURCE	ENGLAND				NORTH AMERICA			UNIVERSAL
	Q	I	G	H	Q	G	H	Q
Sparks 1962	x							x
Sparks 1954	x							x
Turner 1970	x							x
Burchell 1965	x							x
Sparks 1957-58	x	x						x
Miller 1976					x	x		x
Miller 1970					x	x		x
Burchell & Davis 1957	x							x
West et al. 1974	x		x					x
Sparks & West 1964	x	x						x
Getz & Hibbard 1965					x	x		x
Kerney 1957a								x
Kerney 1957b	x			x				x
Tuthill 1963					x	x		x
Karrow et al. 1972					x			x
Zoltai 1969					x		x	x
Davis & Pitchford 1958	x			x				x
Sparks & West 1968	x	x						x
Piechocki 1977								x
Kerney et al. 1964	x			x				x
Kerney 1963	x		x					x

Sparks & West 1970	x	x					x
Stratton 1970b	x		x				x
Sparks & Grove 1961							x
Dimbleby & Evans 1974	x		x				x
Wilson & La Rocque 1973				x		x	x
Cooper 1972	x	x					x
Evans & Valentine 1974	x		x				x
Altena & Kuiper 1945							x
Turk 1966	x		x				x
Wayne 1959a				x	x		x
Wayne 1959b				x		x	x
van der Schalie 1953				x			x
Hibbard & Taylor 1960				x			x
Reynolds 1959				x	x		x
Aukeman 1960				x	x		x
Cornejo 1961				x	x		x
La Rocque & Forsyth 1957				x	x		x
Zimmerman 1960				x	x		x
Mowery 1961				x	x		x
Sheatsley 1960				x	x		x
Clark 1961				x	x		x
van der Schalie 1940				x		x	x
van der Schalie 1939				x		x	x
Dennis 1928				x		x	x
Hubricht 1964c				x			x
Kerney 1976a	x		x				x
Cameron 1978b	x		x				x
Jaeckel 1950							x
Baerreis 1974				x		x	x
Sparks & Lambert 1961	x		x				x
Evans 1966	x						x
Clark 1962				x		x	x
Luttig 1953							x
Pauken 1969				x	x		x
Devore 1975				x	x		x
Evans 1972	x		x				x
Olle 1969				x	x		x
Bickel 1970				x	x		x

Appendix III: Summary statistics for least squares regression equations 1 to 24 describing TAXA on NISP for freshwater, terrestrial and mixed freshwater/terrestrial gastropod samples. (Parameters in natural logarithms)

ENGLAND	QUATERNARY	FRESHWATER INTERGLACIAL	GLACIAL	HOLOCENE
r	0.79551	0.84858	0.88770	0.67473
r^2	0.63284	0.72009	0.78801	0.45527
s^2_{yx}	0.36805	0.18230	0.09145	0.35673
$\bar{x}$	3.8035	4.8133	3.7602	2.7556
s^2_x	5.18473	4.70152	4.45843	3.46146
n	286	122	14	113
a	0.03163	0.50589	0.91160	-0.14523
s^2_a	0.06993	0.09444	0.16983	0.10072
b	0.34918	0.31453	0.26529	0.29217
s^2_b	0.01578	0.01790	0.03972	0.03033
range	0 - 8.5382	0 - 8.5382	1.0986 - 7.2971	0 - 8.2553

ENGLAND	QUATERNARY	TERRESTRIAL INTERGLACIAL	GLACIAL	HOLOCENE
r	0.79796	0.94457	0.68876	0.79791
r^2	0.63673	0.89221	0.47439	0.63667
s^2_{yx}	0.23304	0.12267	0.19072	0.15621
$\bar{x}$	4.6748	2.9065	4.8577	5.0214
s^2_x	2.69026	3.43694	2.13978	1.92710
n	698	107	138	361

a	0.57532	0.24704	0.67969	0.74170
s_a^2	0.05523	0.06318	0.12936	0.07817
b	0.38938	0.54097	0.28260	0.37637
s_b^2	0.01115	0.01835	0.02551	0.01501
range	0 - 8.4202	0 - 6.6477	0 - 8.3092	0.6932 - 8.4202

	MIXED FRESHWATER/TERRESTRIAL			
ENGLAND	QUATERNARY	INTERGLACIAL	GLACIAL	HOLOCENE
r	0.71612	0.81382	0.77961	0.79224
r^2	0.51283	0.66231	0.60779	0.62765
s_{yx}^2	0.26225	0.29138	0.12167	0.16969
$\bar{x}$	5.0817	5.0276	4.9139	5.0984
s_x^2	2.27225	4.38902	2.05492	1.93210
n	731	123	138	363
a	0.77231	0.76201	0.67108	0.71935
s_a^2	0.06665	0.12698	0.10638	0.08230
b	0.34833	0.35936	0.30180	0.38424
s_b^2	0.01257	0.02333	0.02079	0.01558
range	0 - 9.0338	0 - 8.5464	0.6932 - 8.4876	0.6932 - 9.0338

	FRESHWATER		
NORTH AMERICA	QUATERNARY	INTERGLACIAL	HOLOCENE
r	0.84249	0.70069	0.73964
r^2	0.70979	0.49097	0.54707
s_{yx}^2	0.19149	0.19852	0.18867

$\bar{x}$	5.3921	6.3000	2.2005
s_x^2	5.3250	2.3268	2.1618
n	199	149	40
a	0.18717	0.25725	0.10784
s_a^2	0.07901	0.15560	0.12471
b	0.29582	0.28588	0.32048
s_b^2	0.01348	0.02401	0.04730
range	0 - 11.809	0.6932 - 10.739	0 - 6.2265

NORTH AMERICA	TERRESTRIAL QUATERNARY	INTERGLACIAL	HOLOCENE
r	0.84970	0.85064	0.82952
r^2	0.72198	0.72359	0.68810
$s_{y\cdot x}^2$	0.20598	0.20214	0.17163
$\bar{x}$	4.2622	4.3301	3.3837
s_x^2	2.8608	2.7659	1.4595
n	380	299	59
a	0.40170	0.33880	0.37216
s_a^2	0.06319	0.07262	0.16162
b	0.43185	0.43666	0.50492
s_b^2	0.01378	0.01566	0.04503
range	0 - 9.3311	0 - 9.0647	0 - 7.4922

	MIXED FRESHWATER/TERRESTRIAL		
NORTH AMERICA	QUATERNARY	INTERGLACIAL	HOLOCENE
r	0.53666	0.25638	0.65908
r^2	0.28801	0.06573	0.43439
s^2_{yx}	0.21282	0.15102	0.26041
$\bar{x}$	5.3028	5.6466	3.5187
s^2_x	2.27135	1.52054	1.11281
n	458	358	74
a	1.45450	2.08910	0.55437
s^2_a	0.07893	0.09640	0.20787
b	0.19448	0.08348	0.42103
s^2_b	0.01432	0.01668	0.05662
range	0.6932 - 11.834	1.7918 - 10.955	0.6932 - 7.4933

	QUATERNARY		
UNIVERSAL	FRESHWATER	TERRESTRIAL	MIXED F/T
r	0.81160	0.83543	0.67155
r^2	0.65869	0.69794	0.45098
s^2_{yx}	0.29685	0.22501	0.25908
$\bar{x}$	4.3992	4.5340	5.1863
s^2_x	5.6349	3.1421	2.4448
n	537	1134	1251
a	0.12002	0.49539	1.00220
s^2_a	0.04955	0.03870	0.04987
b	0.31855	0.40660	0.04987

s_b^2	0.00991	0.00795	0.00921
range	0 - 11.809	0 - 10.028	0 - 11.834

Appendix IV: Mathematical algorithms necessary for computing the truncated lognormal distribution. The gastropod sample from Level 1 at the Hall Shelter is used as an example. (Details in Hald 1952a, 1952b; Preston 1948, 1962)

Frequency distribution of observed gastropod remains for the sample following Preston (1948):

NUMBER OF INDIVIDUALS PER SPECIES	LOG 2	OCTAVE MID POINT	OBSERVED FREQUENCY
<1			<2
1-2	0-1	0.5	3.5
2-4	1-2	1.5	2.5
4-8	2-3	2.5	0.5
8-16	3-4	3.5	0.5
16-32	4-5	4.5	1.0

Calculation of truncated distribution following Hald (1952a):

t_j = mid point of class

a_j = number of species per class

w_j = computational constant

w_j^2 = squared computational constant

S_o = number of species in the truncated distribution

$\emptyset(z)$ = degree of truncation

$\hat{N}$ = estimated number of species in the universe

y_o = number of species in the modal octave

a = a slope constant in the lognormal curve

R = the number of ocataves from the modal octave

n = number of species in the Rth octave

S = column sum of $w_j a_j$

SS = column sum of $w_j^2 a_j$

t_j	a_j	w_j	w_j^2	$w_j a_j$	$w_j^2 a_j$
0.5	3.5	1	1	3.5	3.5
1.5	2.5	3	9	7.5	22.5
2.5	0.5	5	25	2.5	12.5
3.5	0.5	7	49	3.5	24.5
4.5	1.0	9	81	9.0	81.0
	8.0			26.0	144.0

$S_0 = 8$

$S = 26$

$SS = 144$

$S/S_0 = 26/8 = 3.25$

$$y = \frac{(S_0)(SS)}{2(S^2)} = \frac{(8)(144)}{2(26^2)} = \frac{1152}{1352} = 0.852$$

$z = f(y) = f(0.852) = 0.859$ (Hald 1952b; Table IX)

$g(z) = g(0.859) = 1.804$ (Hald 1952b; Table IX)

$s = (S/S_0)(0.50)(g(z)) = (3.25)(0.50)(1.804) = 2.9313$

$-zs = -(0.859)(2.9313) = -2.518$

$\emptyset(z) = \emptyset(0.859) = 0.805$ (Hald 1952b; Table II)

$$\hat{N} = \frac{100(S_0)}{1-\emptyset(z)} = \frac{(100)(8)}{1-0.805} = 41$$

$y_0 = (0.399)(\hat{N})/s = (0.399)(41)/2.9313 = 5.581$

$a = (0.707)/s = 0.707/2.931 = 0.241$

$$n = (y_0)e^{-(aR)^2}$$

$$n = 5.58e^{-(0.241R)^2}$$

Appendix V: Synthesis of the distribution and ecological requirements of individual gastropod taxa identified for the thesis.

Campeloma Rafinesque 1819

Campeloma decisum (Say) 1817

This species is distributed over most of eastern North America, from Saskatchewan , east to Nova Scotia and Georgia (La Rocque 1968). According to La Rocque (1968:374), this species occurs "in rivers and creeks, on a bottom of sand, mud, gravel and sand, or clay; in shallow water a foot or more deep; generally more abundant in rapid current, but not in riffles or rapids". Additionally, Bickel (1970) notes that the species also occurs in lakes; preferably on very loose sediment. Clarke (1979a) suggests this species is an indicator of eutrophic lake conditions.

Valvata Muller 1774

Valvata bicarinata Lea 1841

This species has a distribution which is very restricted in area and occurs primarily in the eastern portion of the United States (La Rocque 1968). Baker (1928) recorded this species on a variety of substrate bottoms ranging from gravel to mud in very shallow water of several lakes in Wisconsin.

Valvata sincera helicoidea Dall 1905

This species is restricted in its distribution to the northern half of Canada (Clarke 1981). *V. s. helicoidea* is found in oligotrophic and eutrophic lakes (Clarke 1979a). According to Clarke (1981:48), the species lives "in lakes, ponds, slow-moving rivers and streams, and in muskeg pools, usually among aquatic vegetation and on a variety of substrates. Lives at various depths down to 15 m, and is often found in the stomachs of whitefish (Coregonus)".

Valvata tricarinata (Say) 1817

This species has a broad distribution ranging from the Yukon Territory south to Florida (La Rocque 1968). Clarke (1979a) suggests that the species is found in oligotrophic and eutrophic lakes. La Rocque (1968:367) notes V. tricarinata occurs "in shallow water to depths exceeding 9 m.; in lakes and streams, with or without vegetation; on sand, sand and gravel, rock, clay, and mud bottom".

Amnicola Gould and Haldeman 1841

Amnicola limosa (Say) 1817

This species ranges over most of North America, from Alberta east to Newfoundland, and from Texas east to Florida (La Rocque 1968). According to Leonard (1950:12), the "snail is an inhabitant of rivers, creeks, quiet ponds, and small lakes; it seems to thrive both in waters which contain growths of vegetation and those lacking them". Specifically, La Rocque (1968:385) notes the species prefers habitats containing "thick beds of Chara, Potamogeton, Vallismeria, and Elodea. These plants are not used as food by the amnicolid, but they harbor rich colonies of diatoms on which the snail feeds". Wootton (1975:9) suggests the preferred water temperature is 6.7 - 7.0 °C and pH is near 7.95 for this species. According to Clarke (1979a) this species typifies eutrophic lake conditions.

Pleurocera Rafinesque 1818

Pleurocera acutum Rafinesque 1831

This species is restricted in its range to the Great Lakes region and immediate vicinity (Baker 1928). According to Baker (1928:178), *Pleurocera acutum* "appears to be rare on sand and mud bottom in slow current, but common and abundant on rocky shores in a swift current or on shores subject to violent wave action. It is decidedly a shallow water form, becoming rare in water deeper than .5 m". "In rivers, this snail prefers riffles in shallow water" (La Rocque 1968:416).

Goniobasis Lea 1862

Goniobasis livescens (Menke) 1830

The distribution of this species is primarily in the Great Lakes region, occurring as far south as Kentucky (La Rocque 1968). According to La Rocque (1968:422), "this species can live, even thrive, in a variety of habitats, in lakes and rivers, on a variety of bottoms (mud, sand, boulder and gravel) and even on solid rock walls, in swift or quiet water of various depths, even though water level fluctuates as much as four feet within a few hours".

Stagnicola Jefferys 1830

Stagnicola elodes (Say) 1821

This species is primarily northern in its distribution and is common over most of Canada (Clarke 1973). The species occurs in a variety of habitats. It is most commonly found in quiet waters where vegetation is abundant (Baker 1928). According to La Rocque (1968:453), this species occurs "in pondlike areas with thick vegetation; in ponds and sloughs that become more or less dry in summer".

Stagnicola catascopium (Say) 1817

This species is distributed over most of the northern portion of North America, from Great Slave Lake, east to Nova Scotia, and south to Maryland and Iowa (La Rocque 1968). "Characteristic of large lakes and large rivers although also found in smaller bodies of water. Its most frequent habitat is on rocks exposed to waves and currents" (Clarke 1981:136). La Rocque (1968:439) adds that the "species is typically a river mollusk living on gravel, stones, and floating logs in shallow water 1 to 2 feet deep, current rather rapid". In terms of lake conditions, Clarke (1979a) suggests the species is an indicator of oligotrophic and mesotrophic stages of development.

Stagnicola arctica (Lea) 1864

This species is restricted in its distribution to the northern half of Canada (Clarke 1981). S. arctica can be found "in lakes, ponds, rivers, streams, ditches, and muskeg pools. Vegetation abundance and bottom sediments are variable" (Clarke 1981:134). Although most common in eutrophic lakes, the species also occurs in mesotrophic lakes (Clarke 1979a).

Fossaria Westerlund 1885

Fossaria parva (Lea) 1841

This species is distributed over most of North America, from the Yukon Territory south to Texas (La Rocque 1968). La Rocque (1968:478) notes *F. parva* "lives in wet, marshy places, generally out of the water, on sticks, stones, or muddy flats. It is more prone to leave the water than any other species of the family".

Physa Draparnaud 1801

Physa jennessi Dall 1919

This species is restricted in its distribution to the northern half of Canada (Clarke 1981). This arctic snail occurs "in small lakes, ponds, woodland pools, muskeg pools, small pools on top of flat boulders, and slow-flowing streams. Vegetation present in some habitats but absent in others; substrates are rock and mud" (Clarke 1981:160).

Helisoma Swainson 1840

Helisoma trivolvis (Say) 1817

This aquatic snail has an exceptionally wide distribution ranging from the Arctic coast in Alaska, south to the state of Mississippi (La Rocque 1968). La Rocque (1968) considers it a hardy species with known occurrences in lakes, quiet rivers and even temporary ponds. Clarke (1979a) suggests the species is a common element of mesotrophic and eutrophic lakes. According to Leonard (1950:16), "Helisoma trivolvis is an inhabitant of quiet or somewhat stagnant waters. It flourishes in ponds and sloughs, even though they may be choked with vegetation or polluted with decaying organic materials. It is invariably absent from flowing streams, or restricted to quiet coves along the stream course".

Gyraulus Agassiz in J. de Charpentier 1837

Gyraulus parvus (Say) 1817

This species occurs over most of North America east of the Rocky Mountains, from Alaska south to Florida (La Rocque 1968). La Rocque (1968:491) states that this species is usually "found in quiet bodies of water, mainly those of small size, on mud, sandy mud, sand, gravel, or boulder bottom; also on logs and vegetation, in shallow water a foot or more, up to 4 feet deep. Its ideal habitat seems to be vegetation, in protected situations". In Kansas, G. parvus "is frequent on or among aquatic plants such as Chara, Typha, Spirogyra, and duckweed, and occurs on submerged blades of living and dead grasses or on dead tree leaves in water. G. parvus is often found in the larger lakes on floating, partly water-logged pieces of driftwood that have been washed up along shore" (Leonard 1959:61). In Nebraska, Taylor (1960) records the species in seepages near streams, as well as temporary ponds. "In Mead County, Kansas, and Harper County, Oklahoma, this species was collected from rooted vegetation growing in permanent water situations" (Miller 1966:233). Wootton (1975:11) states the species "has a pH range of 7.0 - 8.16 and a fixed carbon dioxide range of 8.16 - 30.56 ppm". Clarke (1979a) suggests the species indicates mesotrophic to vernal lake conditions.

Gyraulus circumstriatus (Tryon) 1866

This species is distributed over most of North America, from the Yukon Territory east to Ontario, and south as far as Arizona and Illinois (La Rocque 1968). This aquatic snail is found in "small vernal habitats such as woodland pools, marshes, roadside ditches, prairie ponds, and intermittent streams. Vegetation is ordinarily thick, and substrates are commonly mud" (Clarke 1981:176).

Gyraulus deflectus (Say) 1824

This species is distributed over most of Canada and the northern portion of the United States (La Rocque 1968). Clarke (1981:178) suggests the species is found "in all kinds of permanent-water, eutrophic habitats. The usual substrate is mud. Commonly lives on vegetation but is occasionally found on the bottom".

Polygyra Say 1818

Polygyra sp.

Members of the family Polygyridae occur widely over most of North America. Except for several species of the genus Ashmunella, all inhabit humid country. According to Leonard (1950:35), "with few exceptions, they are absent where the average annual rainfall is below 30 inches, and most species occur where annual precipitation exceeds this amount". Similarly, all but several species of Ashmunella are non-burrowing snails. Most species live under stones and dead wood/leaves. Diet consists primarily of fungal mycelia (Pilsbry 1940).

Stenotrema Rafinesque 1819

Stenotrema stenotrema (Pfeiffer) 1842

This species ranges over most of the southeastern portion of the United States, from Missouri to Virginia and south to Louisiana (Pilsbry 1940). In Kentucky, S. stenotrema is known to occur on forested slopes and creek bottoms with high calcium content (Conkin 1957). According to La Rocque (1970), it occurs in red and black oak communities in Tennessee; usually on bluffs with rocky rubble. In Georgia, this species was found on forested slopes. Leonard (1959:84) notes the "snail is solitary; only one or two individuals are usually found together under chips, bark, logs, and similar debris".

Stenotrema hirsutum (Say) 1817

This species has an exceptionally wide distribution in eastern North America, ranging from Wisconsin, east to New York, and south to Georgia and the state of Mississippi (Pilsbry

1940). In Ontario, Oughton (1948) observed this species as abundant in wet locations adjacent to streams. Ingram (1944) notes that S. hirsutum in the state of New York is vegetatively associated with beech-yellow birch stands; occurring under stones on floodplains. Rehder (1949) collected this snail among stones in North Carolina, while Grim found it in quarries and woods in Virginia (La Rocque 1970). As noted by La Rocque (1970), in Virginia the species prefers very steep hillsides, dry oak ridges and southern exposures.

Mesodon Rafinesque 1821

Mesodon thyroidus (Say) 1816

This species is distributed over most of eastern North America, from Ontario and Massachusetts to Kansas, and Texas to the Gulf of Mexico (Pilsbry 1940). "This forest snail is found on and under rotten logs, smaller pieces of wood and in litter. (It) seems to be closely associated with floodplains and their margins in Kansas, but has been reported from drier situations in Indiana" (Leonard 1959:90). According to Call (1900), in marshy areas of Indiana, this species is frequently found in trees several feet above the ground. In Ontario this species was found by Oughton (1948) in damp deciduous woodlands high in calcium content. Conkin (1957) recorded this species on forested and bushy slopes in Kentucky, while Rehder (1949) found it among stones and rotting timbers in South Carolina. In Virginia, Burch (1955) noted its preference for oak woodlands, while La Rocque (1970) suggests floodplain preference in

Virginia, and bluffs and hardwood forests in Tennessee.

Mesodon _appressus_ (Say) 1821

This species is restricted in its distribution to an area within Indiana, Ohio, Kentucky, Tennessee and Alabama (Pilsbry 1940). According to Pilsbry (1940), _M._ _appressus_ usually occurs in weedy, calcareous soils in the state of Alabama, but it is known from weed covered gravel hills in Indiana. In Tennessee, the species has been observed on foothill regions covered in hardwood forests and logs which are underlain with rocky rubble (La Rocque 1970). Typical in the cities of Virginia and abandoned coal mines of West Virginia, this species appears to favor culturally disturbed habitats (La Rocque 1970).

Mesodon sp.

The genus occurs over most of eastern Canada and United States; as far west as Nebraska and Texas (Pilsbry 1940). _Mesodon_ _thyroidus_, _Mesodon_ _inflectus_ and _Mesodon_ _clausus_ are all forest species (Leonard 1959). _M._ _thyroidus_ is found associated with litter, rotten logs and pieces of wood, occasionally near marshy areas and floodplain margins (Leonard 1959). In Illinois, Pilsbry (1940) notes _M._ _thyroidus_ feeding on fungi, mildewes and slime molds. Baker (1939) notes _M._ _inflectus_ to be a gregarious, leaf litter species in Illinois.

Triodopsis Rafinesque 1819

Triodopsis _tridentata_ (Say) 1816

This species is distributed throughout eastern North

America, from Ontario south to Mississippi, and west as far as Illinois (Pilsbry 1940). "*T. tridentata* is more abundant on limestone soils, but it lives everywhere, wherever there is some shade, with moderate moisture, herbage, dead leaves or wood shelter. Though hilly country is preferred, it is not found in the higher Appalachians " (Pilsbry 1940:796). Oughton's (1948) observations in Ontario indicate damp and dry habitats in open woodlands are commonly exploited by this species. According to La Rocque (1970), this species is found in red and black oak forests on hilly terrain in Tennessee and hillsides in Pennsylvania. In the state of New York, Ingram (1944) notes the species is associated with sycamore and beech-yellow birch woodlands. Additionally, he notes that *Triodopsis tridentata* occurs abundantly in maple and hemlock stands, and is not very tolerant of cultural disturbance, given its scarcity on grass covered or cultivated fields.

Triodopsis denotata (Ferussac) 1821

This species has a wide distribution in eastern North America, from Ontario south to Mississippi, and west as far as Illinois (Pilsbry 1940). In Jefferson County, Ohio, *T. denotata* was observed in a locality of steep ledges, partly wooded and adjacent to a stream (La Rocque 1963b). The snail lives under leaf mold, bark and logs (La Rocque 1963b). The most northern record for this species appears to be Russel County, near Casselman, Ontario (La Rocque 1964). In New York state, Ingram (1944) associated this species with sycamore and beech-yellow birch woodlands, and commented that it rarely occurs in any numbers in most locales.

Triodopsis albolabris (Say) 1816

This species is restricted in its distribution to eastern North America, from Quebec and Ontario south to Georgia, and west as far as the Mississippi River (Pilsbry 1940). "This snail is usually more abundant and somewhat more solid on limestone terrains" (Pilsbry 1940:836). Although essentially a forest snail, it "shows a distinct adaptiveness to conditions brought about by deforestation, small individuals of T. a. albolabris being reported from grasslands and sandy areas" in Ontario, Michigan and Indiana (Leonard 1959:98). Vegetational preferences of the species are deciduous stands, primarily beech-maple and maple associations (Ingram 1944). In Kentucky, Conkin (1957) observed the species on forested and bushy slopes. T. albolabris is one of the most common and abundant of the forest snails and appears to adapt well to man's interference, as evident by its high presence under boards at a settlement in North Carolina (Rehder 1949).

Euconulus Reinhardt 1883

Euconulus fulvus (Muller) 1774

This species has a Holarctic distribution and is generally absent in the southern United States. E. fulvus lives in well-shaded areas amid damp leaves. The species is also common in fluvial drift debris (Pilsbry 1946). In Michigan, Miller (1966) collected specimens among scattered shrubs and high grass in floodplain marsh areas. According to Leonard (1952:19), this species "lives only where good cover of organic debris is available". In terms of vegetative types, the order of habitat preference for this species is as follows: trembling aspen, lodgepole pine-trembling aspen, mixed deciduous-coniferous, mixed deciduous, englemann spruce-lodgepole pine-aspen, and finally, grassland associations (Karlin 1961). This species appears to be tolerant of human interference, given its occurrence in settlements of New York state (Ingram 1944) and open fields and pastures in Ontario (Oughton 1948).

Euconulus chersinus (Say) 1821

This species occurs in the area bounded by Florida, New Jersey, Illinois and Louisiana (Pilsbry 1946). According to Leonard (1959:111), *E. chersinus* "is to be found in and about decaying wood, under sticks, logs, the loosened bark of fallen trees, beneath stones and in leaf litter on the forest floor". Leonard (1959) also notes that the species is restricted to humid/moist habitats but can survive lengthy periods of drought. In Illinois, this species "is found in isolated woodlands containing oak, cherry, hickory or ironwood" (Baker 1939:76). Association to oak-hickory stands by this species was also noted by Archer in North Carolina (La Rocque 1970).

Euconulus sp.

Holarctic in distribution, the genus is common to high latitudes (Pilsbry 1946). Members of the genus are all small woodland snails. It is a rare event to find more than two individuals of this species in one spot (Baker 1939). However, as noted by La Rocque (1970:608), the small size of the genus "makes it inconspicuous but its true abundance is revealed when leaf mold is sifted".

Guppya Morch 1867

Guppya sterkii (Dall) 1888

This species is restricted to the far eastern portion of North America, ranging west as far as Ontario, Ohio, Kentucky and Louisiana (La Rocque 1970). Although commonly associated with moss and small bushes on grassy slopes (La Rocque 1970), its confinement to Paleozoic based terrains in Ontario indicates it is a calciphile (Oughton 1948).

Nesovitrea C.M. Cooke 1921

Nesovitrea electrina (Gould) 1841

This species ranges over most of North America, from Alaska south to New Mexico, and east to Maryland (Pilsbry 1946). "This snail has been found in both upland wooded areas and along the margins of streams. It seems to require a fairly moist environment, not occurring out in the open grasslands as does Zonitoides arboreus with which electrina is frequently elsewhere associated" (Leonard 1959:112). "R. electrina is common in the woodlands of eastern Kansas, where the annual rainfall is generally more than 35 inches but it declines in frequency of occurrence toward the more arid Plains Border province" (Leonard 1950:37). According to Leonard (1959:112), "it is to be looked for under sticks, logs, rocks, and in crevices of started bark as in leaf litter". In Ontario, Oughton (1948) emphasizes its occurrence is restricted to river and lake margins. One can conclude that its distribution is sporadic (Baker 1939). In terms of vegetative types, the order of habitat preferences of this species is as follows: trembling aspen, mixed deciduous-coniferous, and finally, englemann spruce-lodgepole pine-aspen associations (Karlin 1961).

Nesovitrea binneyana (Morse) 1864

The distribution of this species is poorly documented, although La Rocque (1970) records its distribution as ranging from Alberta and Colorado, east to Ontario and Kentucky. Clark (1961:25) notes R. binneyana "is common in forests of birch, aspen, maple, cedar, fir, hemlock, spruce, and pine. Here it is found in several different situations but is most common under forest debris, at the base of stumps, under logs, and under the loose bark of fallen trees. This species also lives on lowlands which border lakes". In terms of vegetative types, this species prefers trembling aspen and lodgepole pine-trembling aspen associations (Karlin 1961).

Retinella "Shuttleworth" Fischer 1877

Retinella wheatleyi (Bland) 1833

This species is distributed widely over eastern North America, ranging from New York, Ontario and Michigan, south to Alabama and South Carolina (Pilsbry 1946). "Even in the spring it was rare except in a shallow valley on the west-facing (more humid) slope of the ridge, where one or two individuals per square meter were obtained under decaying leaves in the oak-chestnut woods" of Tennessee (Baker quoted in Pilsbry 1946:273).

Retinella indentata (Say) 1823

This species occurs over most of the eastern United States (Pilsbry 1946). Commonly associated with *Nesovitrea electrina* and *Zonitoides arboreus*, *R. indentata* "is found under and in rotting logs, leaves and other forest debris in both upland and forest situations" (Leonard 1959:114). Although primarily a damp woodland species, Gibson (1967:21) notes its occurrence "in quarries, sandy outwash plains, along railroad tracks, pine forests, and cliffs and bluffs along creeks". Additionally, Clark (1961) suggests the species prefers slightly drier conditions than that favored by *N. electrina*. In Illinois, its favorite habitat "is in woodlands of oak, elm, maple and hickory" (Baker 1939:71).

Retinella sculptilis (Bland) 1858

This species is distributed over the southeastern portion of the United States (Pilsbry 1946). Nothing is known of this species ecological preferences or requirements, although as with other *Retinella* species, it is probably rare in its occurrence and usually associated with aspen vegetation along waterways.

Retinella sp.

There are some 20 North American species ranging from the Arctic to Mexico, most of which occur around the Appalachian region (Leonard 1950). "The animals of this genus are inhabitants of relatively humid woodlands" (Leonard 1950:36). Following Karlin (1961), this genus is typically found in mixed deciduous-coniferous vegetation associations.

Mesomphix Rafinesque 1819

Mesomphix cupreus (Rafinesque) 1831

This species ranges in distribution from Ontario south to Alabama and west as far as Missouri (Pilsbry 1946). "Mesomphix cupreus lives in densely shaded woodland on hillsides, and is usually found partly buried in the damp humus, under a layer of dead leaves" (Pilsbry 1946:336). In Illinois, it is typically found "in forests of oak, elm, hickory, walnut and ironwood" (Baker 1939:66). Similarly, Ingram (1941) found the snail in pure maple stands in New York state and noted that individuals tend to cluster in their distribution, prefering cool habitats with dense overhang.

Mesomphix rugeli (W.G.Binney) 1879

Pilsbry (1946) describes the distribution of M. rugeli as Virginia, North Carolina, and Tennessee. Ecological data is lacking but given habitat preferences of other Mesomphix spp., this species also prefers damp, well-shaded wooded areas, usually on hillsides (Leonard 1959).

Mesomphix vulgatus H.B.Baker 1933

This species has a wide distribution over eastern North America, including Ohio, Indiana, Illinois, Kentucky and Tennessee in the northwestern portion of its range (Pilsbry

1946). Pilsbry (1946:325) citing Daniels suggests the species is found "in dry upland woods, under logs". In North Carolina, the species was observed on high banks covered in hardwoods, while populations in Georgia were recorded in culturally disturbed surroundings (La Rocque 1970).

Mesomphix friabilis (W.G. Binney) 1857

This species is restricted in its range to the southeastern portion of the United States (La Rocque 1970). Ecological requirements of this taxon are basically unkown, although La Rocque (1970) mentions that specimens have been recorded on bluffs along rivers.

Mesomphix sp.

Members of this genus occur over most of eastern North America. Generally, these snails occur in regions containing deciduous forest and moderate to high humidity.

Paravitrea Pilsbry 1898

Paravitrea capsella (Gould) 1848

This species occurs in the eastern United States from southern Illinois and Indiana down to northern Alabama, east to North Carolina (Pilsbry 1946). According to Leonard (1959: 115), P. capsella "is a woodland snail found under dead leaves, loose bark and underneath fallen branches". Rarely does this species occur in oak, hickory, elm or pine woodlands (Baker 1939). Additionally, La Rocque (1970) notes this species is found on high bluffs in Virginia.

Paravitrea sp.

Most members of the genus Paravitrea are restricted in their distribution to the eastern portions of Canada and the United States (Pilsbry 1946). In Virginia, the type species Paravitrea capsella is common on bluffs along rivers (Hubricht 1952). In Ontario, Paravitrea multidentata occurs primarily in damp deciduous woodlands (Oughton 1948). All members of the genus are woodland snails and are typically associated with leaves, loose bark and logs (Leonard 1959).

Hawaiia Gude 1911

Hawaiia minuscula (Binney) 1840

This species is widely distributed over most of North America (Pilsbry 1946). "Hawaiia miniscula (sic) is an inhabitant of humid situations, where it lives in leaf mold, on and beneath the bark of trees, among mosses, and beneath fallen logs, or beneath stones. It is capable, in spite of its habitat preferences, of withstanding long periods of drought and high temperature" (Leonard 1950:36). Because this species is so adaptive "its presence in a faunal assemblage means little" (Leonard 1952:20). This species is commonly found in oak, hickory and sycamore woodlands (Baker 1939). Karlin (1961) generalizes the preferred vegetative type as an englemann spruce-lodgepole pine-aspen association. La Rocque (1970) cites several examples from Virginia and South Carolina that indicates this species is more than tolerant of human disturbance and interference.

Gastrodonta Albers 1850

Gastrodonta interna (Say) 1822

This species ranges over most of the southeastern portion of the United States, from Ohio and Indiana south to Georgia (Pilsbry 1946). In the hardwoods of North Carolina, this species is "the most common and and universally distributed zonitid in this locality. It is of great importance as an indicator of former fires, for it is favored by fires, and appears as one of the species of the fire succession group, is common under charred logs, and is equally at home in oak-pine woods as it is in oak-logs" (Archer quoted in La Rocque 1970: 641).

Ventridens Binney 1863

Ventridens gularis (Say) 1822

This species occurs in the far eastern portion of the United States, ranging from Indiana and Ohio, south to Georgia and Louisiana (Pilsbry 1946). In North Carolina, V. gularis occurs in hardwood forests associated with leaf mold and acidic soils (La Rocque 1970). In Georgia, this species has been recorded on high bluffs away from pine trees (La Rocque 1970).

Ventridens intertextus (Binney) 1841

This species has an eastern distribution in North America, from Ontario south to Louisiana, bordered on the west by the Mississippi River (Pilsbry 1946). According to Oughton (1948), in Ontario, this species favors damp deciduous woodlands. A prey species of the carabid Calosoma, La Rocque (1970) describes V. intertextus as common but sporadic on forested slopes, rare to absent in open fields and abundant in association with A. anguispira on floodplains.

Ventridens demissus (Binney) 1843

This species occurs in the eastern half of the United States, from Michigan south to Louisiana and Florida (Pilsbry 1946). La Rocque (1970) suggests the species is common on cultivated fields as well as oak-hickory woods. This synanthropic snail has been recorded in small concentrations under logs and in common gardens. Additionally, Clark (1961) notes the species has been recorded on river bluffs in Illinois.

Ventridens ligera (Say) 1821

This species has an eastern distribution in North America, from Ontario south to Florida, and as far west as Oklahoma (Pilsbry 1946). According to Leonard (1959), this species prefers moist and marshy habitats, high in leaf mold, fallen timber and debris. Baker (1939) suggests the species is more common on hill and bluff regions in forest habitats dominated by elm, oak, dogwood, locust and sumac. From his observations in Tennessee and Pennsylvania, La Rocque (1970) adds sloped terrains covered in hardwood forests as suitable habitats for this species.

Ventridens sp.

Distribution of this genus is restricted to eastern Canada and United States (Pilsbry 1946). Members of the genus prefer moist situations along floodplains and uplands. In Kansas, for example, _Ventridens ligera_ has been recorded in marshy areas rich in timber and leaf mold (Leonard 1959).

Zonitoides Lehmann 1862

Zonitoides arboreus (Say) 1816

This species has an exceptionally wide distribution and is one of the most common snails in North America. "The snail is found in wooded areas, on bluffs along streams, in grassland and under stones" (Leonard 1959:123), "and other cover affording protection from the sun, and providing at least moderate moisture" (Leonard 1950:37). Despite its varied habitats, one can attribute "its scarcity in certain localities to absence of decaying logs" (Leonard 1959:123). This species is primarily gregarious (Clark 1961), which accounts for its high frequency in certain fossil assemblages. In terms of vegetative types, the order of habitat preferences of this species is as follows: mixed deciduous-coniferous, mixed deciduous, trembling aspen, lodgepole pine-trembling apsen, englemann spruce-lodgepole pine-aspen, and finally, lodgepole pine associations (Karlin 1961). Basically, this species can be considered synanthropic, given its high tolerance of human interference.

Zonitoides sp.

"_Zonitoides_ is holarctic in distribution, occurring in most temperate parts of the northern continents ... (and) has become adapted to a wide range of habitat situations, from subarctic to and United States (Pilsbry 1946). Members of the genus prefer moist situations along floodplains and uplands. In Kansas, for example, Ventridens ligera has been recorded in marshy areas rich in timber and leaf mold (Leonard 1959).

Zonitoides Lehmann 1862

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Zonitoides sp.

"Zonitoides is holarctic in distribution, occurring in most temperate parts of the northern continents ... (and) has become adapted to a wide range of habitat situations, from subarctic to tropical, throughout its great range" (Leonard 1950:37).

Striatura Morse 1864

Striatura sp.

Members of this Nearctic genus occur over most of eastern North America (Pilsbry 1946). Commenting on *Striatura milium*, Pilsbry (1946:496) notes that he "found it most frequently on northern slopes with chestnut, beech or even oak timber ... among dead leaves in the woods".

Anguispira Morse 1864

Anguispira alternata (Say) 1816

This species is common and widely distributed over eastern Canada and United States (Pilsbry 1946). Although typically a woodland/floodplain species (Leonard 1952), it is also observed "on uplands in appropriate situations, such as under logs, brush piles, boards, rock piles and about rocky ledges" (Leonard 1959: 130). In Illinois, this species has been collected high up in trees by Baker (1939). This species seems to prefer open woodlands or secondary clearings with extensive low cover (Bickel 1970). A prey species of the short-tailed shrew (La Rocque 1970), Oughton (1948) describes *A. alternata* as an ubiquitous, prolific and hardy snail.

Anguispira kochi (Pfeiffer) 1845

Recorded as far north as Ontario, *A. kochi* is primarily restricted in its distribution to the areas bordering the Mississippi drainage system (Pilsbry 1948). This species is not as adaptive as A. alternata, but does occur on calcareous soils near sparse wooded areas (La Rocque 1970). In Kentucky, Conkin (1957) recorded this species on calcareous soils on forested and bushy slopes and creek bottoms.

Discus Fitzinger 1833

Discus cronkhitei (Newcomb) 1865

This species is known to occur from Alaska south to California, and east to Maryland and Labrador (Pilsbry 1948). "In the east it lives in humid forests, under dead wood, and among rotting leaves and grass in rather wet situations. It is a common snail in the Canadian and Transition faunas, and occurs sporadically in the Carolinian" (Pilsbry 1948:604). In the south, D. cronkhitei occurs at altitudes between 7,000 and 8,000 feet (Leonard 1950). Bickel (1970:30) notes D. cronkhitei "occurs both in dry areas and moist situations such as along the margins of lakes". In terms of vegetative types, the order of habitat preferences of this species is as follows: trembling aspen, lodgepole pine-trembling aspen, mixed deciduous, and finally, grassland associations (Karlin 1961). Besides damp deciduous woodlands, Oughton (1948) has observed this species in Sphagnum bogs.

Discus patulus (Deshayes) 1830

This species has an exceptionally broad distribution over eastern North America, ranging north to Ontario, south to Florida and west as far as Iowa (Pilsbry 1948). Pilsbry (1948:609) notes that the species is often abundant and "lives in the rich mould around rotting logs, and under their loose bark, or burrowing in the soft, rotten wood". In Ontario, the species is typically found in damp deciduous woodlands (Oughton 1948). In North Carolina, *D. patulus* has been observed in leaf mold associated with rocks (La Rocque 1970). Ingram (1944) notes that the species is vegetatively associated with beech-yellow birch and sycamore.

Discus sp.

The genus *Discus* contains a group of small snails with a Holarctic distribution (Leonard 1950). Members of the genus are fairly common in Canada and United States and tend to prefer moist to damp wooded conditions (Bickel 1970).

Helicodiscus Morse 1864

Helicodiscus parallelus (Say) 1821

This species occurs in northeastern North America from Newfoundland to Alabama, west to Texas and north to Nebraska (Leonard 1950). "It lives on decaying wood in shady or humid places, also on damp leaves" (Pilsbry 1948:627). In Indiana, this species is most commonly found in floodplain regions (Leonard 1959). "It occurs near lakes and in bogs and swampy areas" (Bickel 1970:31). Given this species' preference for woodlands, it rarely occurs in open areas but will be found in secondary forest growth occasionally (Baker 1939). In New York state, Ingram (1944) recognized the species as the dominant member of bog associations.

Succinea Draparnaud 1801

Succinea grosvenori Lea 1864

This species is distributed widely over most of North America, ranging north as far as Great Slave Lake and south to Texas (Pilsbry 1948). Basically a xeriphilous snail, *Succinea grosvenori* is "tolerant of a wide range of temperature and other factors of environment, but thrives where there is considerable moisture during some seasons of the year. It is frequently found on mud flats near ponds" (Leonard 1950:24). Karlin (1961) generalizes on the preferred vegetative types of this species as being an englemann spruce-trembling aspen association. Mozley's (1928) records from Manitoba indicate this species can withstand severe winters, while La Rocque's (1970) observations from Arizona reflect a high temperature tolerance for the snail. Nonetheless, the species is distinctly xeric.

Succinea avara Say 1824

This species is widely distributed over most of North America, ranging from the Mackenzie area south to Florida (Pilsbry 1948). "*S. avara* is usually found on vegetable debris thrown up on muddy shores, or crawling on the muddy banks of ditches, often exposed to the sun; also in swampy places in pastures" (Pilsbry 1948:839). "It is found also in upland habitats, living under leaves, fallen logs, or beneath stones, often in association with various Pupillidae" (Leonard 1950:23). In Illinois, the habitats of this species "include oak, elm, walnut and ironwood in hillside regions; oak, elm, birch, beech and maple in floodplain regions" (Baker 1939:124). In terms of vegetative types, this species prefers trembling aspen and lodge pole pine-trembling aspen associations (Karlin 1961). Several other observations confirming exceedingly moist habitats from Wisconsin, Manitoba and Michigan are outlined by La Rocque (1970).

Strobilops Pilsbry 1893

Strobilops aenea Pilsbry 1893

Pilsbry (1948) gives the distribution of S. aenea as being eastern North America from southern Ontario south to Louisiana. Typically associated with Strobilops labyrinthica, S. aenea and S. labyrinthica are the most common and abundant species of Strobilops in eastern United States (Pilsbry 1948). According to Baker (1939:114), S. aenea is an uplands species found "in forests of oak, elm, hickory, dogwood, walnut, sassafras, and ironwood. Only rarely is it found in a floodplain valley and then only when the situation is dry". It is found primarily under decaying wood and fallen trees (Clark 1961).

Gastrocopta Wollaston 1878

Gastrocopta armifera (Say) 1821

This species is widely distributed over eastern North America (Leonard 1959), with isolated records as far west as Alberta and Colorado (Pilsbry 1948). "Gastrocopta armifera is a gregarious species occurring commonly on wooded slopes, near or removed from a stream. It is to be found under dead wood, limestone rocks, or light cover of leaf mold or other debris"

(Franzen and Leonard 1947:329). "In northern Nebraska it was found under logs, barks, and stones in moist grass around seepages" (Taylor 1960:72). Nave (1969:28) citing La Rocque notes, "in central Ohio it is very abundant in disused quarries and in crevices formed by bedding planes of limestones along roadsides, river banks and hillside gullies, in some cases in exposed situations without protective cover. It is the commonest pupillid in stream-drift collections in Ohio". Hibbard and Taylor (1960) also note _G. armifera_ is abundant in localized patches near dead wood or single trees in southwestern Kansas. In drier locations, _G. armifera_ is found in association with _Gastrocopta cristata_ and _Pupoides albilabris_ (Miller 1966:241).

Gastrocopta contracta (Say) 1822

This species occurs over most of eastern Canada and United States, from Manitoba and Ontario south to Mexico (Pilsbry 1948). _Gastrocopta contracta_ is commonly found in association with _G. armifera_. However, "_Gastrocopta contracta_ does not seem to be so abundant at any one locality nor to occur in so dry a situation as _G. armifera_" (Leonard 1959:174). Hibbard and Taylor (1960) give its habitat as shaded areas near water. According to Leonard (1950:31), it "is an inhabitant of wooded slopes, where it lives under leaf mold, the bark of fallen logs, or stones". Similarly, Clark (1961:27) suggests _G. contracta_ "is most numerous under forest litter in poorly drained areas near the bottom of hillsides". "It is locally more abundant where loose limestone rock provides cover" (Leonard 1950:31).

Gastrocopta pentodon (Say) 1821

This species has an exceptionally wide eastern distribution in both Canada and the United States (Pilsbry 1948), more so than any other North American *Gastrocopta*. "It lives on wooded hillsides or in well-drained groves, among leaves in the underbrush" (Pilsbry 1948:888). Leonard (1959:176) also notes the species occurs "under suitable cover in grasslands". Baker (1939:100) emphasizes its absence in wet situations, and states it is associated with forests "of oak, cherry, ironwood and basswood" on hillsides.

Gastrocopta corticaria (Say) 1816

This species is distributed from Maine to Minnesota and south to Louisiana (Pilsbry 1948). According to Leonard (1959: 178), "*G. corticaria* has been found in the crevices of rotting logs, under sticks and stones, and on the bark of living trees". Pilsbry (1948:894) notes, "*G. corticaria* is often found crawling upon trees a foot or two from the ground. While generally distributed, it rarely occurs in abundance". Oughton's (1948) observations in Ontario suggest a strong reliance on highly calcareous soils by this species, while La Rocque (1970) suggests hardwood covered moraines as typical habitats in Michigan.

Gastrocopta procera (Gould) 1840

This species is distributed in the eastern United States, from South Carolina to Maryland and west to Kansas (Pilsbry 1948). "*Gastrocopta procera* is typically an inhabitant of timbered slopes near streams, where it lives in leaf mold, beneath fallen logs or loosened bark, or beneath stones, but it is sometimes found living in meadows in dead grass" (Leonard 1950:32). "Its general distribution in Kansas indicates an ability to withstand periods of summer drought" (Franzen and Leonard 1947:342). In agreement, Leonard (1950:32) states, "its wide distribution indicates an ability to tolerate wide extremes of temperature and humidity".

Pupoides Pfeiffer 1854

Pupoides albilabris (C.B. Adams) 1841

This species has an eastern distribution in North America, from Maine and Ontario south to Cuba and as far west as Colorado (Pilsbry 1948). According to Franzen and Leonard (1947:371), P. albilabris is "tolerant of high temperatures and drought, is found in woodlands, in deep grass, or even among the roots of short grass in unshaded areas". "Populations are usually more dense in limestone areas than elsewhere. It does not ascend to high elevations in mountains" (Leonard 1950:29). "This common snail prefers limestone soils,....in well-drained but often sunny places; following rains it is sometimes found on trees a few feet from the ground" (Pilsbry 1948:923). "To the east of Kansas in Indiana and Illinois this snail lives under sticks, logs and leaf-litter in wooded areas as well as in drier situations such as open pastures, railroad embankments and rocky, open country" (Leonard 1959:182; Baker 1939). Burch's (1955) records in Virginia associate this species with oak and maple trees.

Vertigo Muller 1774

Vertigo tridentata Wolf 1870

This species ranges in its distribution from Maine to Ontario, south to Kansas and Kentucky (Leonard 1959). Wolf quoted by Pilsbry (1948:966) states it is "abundant in shady copses on green weeds, climbing as high as three feet from the ground". "It is not a common species, and little is known of its ecological requirements" (Leonard 1950:27). In general, however, this species can be considered a grass or weed fauna (Baker 1939).

Vertigo modesta (Say) 1824

This species has a northern distribution ranging from Labrador to Alaska, and south as far as Missouri and Kansas (Pilsbry 1948). "Vertigo modesta thrives in climates which are cooler and more humid than that now prevailing in the midcontinent region; it is abundantly present in Alaska" (Leonard 1950:27). "In Ontario this species is found in wet locations, such as margins of ponds, streams, and marshes" (Oughton 1948:98). In terms of vegetative types, the order of habitat preference of this species is as follows: englemann spruce-trembling aspen, englemann spruce-lodgepole pine-aspen, trembling aspen, and finally, lodgepole pine-trembling aspen associations (Karlin 1961).

Vallonia Risso 1826

Vallonia gracilicosta Reinhardt 1883

This species is distributed over most of central North America, from New Mexico (high elevations) north to southern Alberta (Leonard 1952; Pilsbry 1948). "*Vallonia gracilicosta* is an inhabitant of situations where leaf mold, stones, and dead grass offer protection. The animals burrow into the earth where the soil is not too compact" (Leonard 1950:33). "In northern Nebraska *Vallonia gracilicosta* occurred with *V. parvula* on moist leaf mold under logs, bark, and stones in wooded areas" (Hibbard and Taylor 1960:138). In terms of vegetative types, the order of habitat preference of this species is as follows: englemann spruce-lodgepole pine-aspen, lodgepole pine-trembling aspen, and finally, trembling aspen associations (Karlin 1961). Shimek (1930b) concluded that the species is one of the most common land snails of the prairie environment.

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