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BIOVOLUME REVISITED: A RELATIVE DIVERSITY INDEX FOR PALEOECOLOGICAL ANALYSES[1]

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Abstract. A new application of the biovolume abundance index is proposed for relative diversity demography in paleoecological analyses. Use of this technique will improve confidence in data validity and solve the following inadequacies of other numerical census techniques: all groups are treated equally, samples from different lithologies can be meaningfully compared, colonial and solitary organisms are treated equally, whole and fragmentary fossils are treated equally, and time averaging effects are assumed. Biovolume is the paleontological analog of biomass, and it is a measure of the relative amount of energy expended by organisms to secrete skeletal material that has been incorporated into the rock record.

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During the past 15 yr, statistical treatment of paleoecological data has become quite fashionable. Cluster analysis (Valentine and Peddicord 1967, Hohn 1976), factor analysis (McGhee 1976), and canonical variate analysis (Buzas 1972) are a few techniques that have provided insight to paleoecological studies.

In evaluating such studies, concerns for data base validity can be raised. Was sampling and sample evaluation completed in a statistically random manner, were all groups treated with equal rigor, and how comparable are samples from different lithologies? In analyses that utilize relative abundance data, additional problems arise. How were colonial organisms counted, how were fragmentary organisms counted, and what effect does time averaging and variable life spans among different species have? These and other problems may prejudice paleoecological data. The reliability of any paleoecological study is a function first of the fidelity of the primary data collection and only secondly of factors such as the mechanical manipulation and interpretation of quantitative techniques.

The paper will outline a new means by which to use the biovolume relative diversity index introduced by Walker (1972a, 1972b). Many of the problems mentioned above can be overcome with this biovolume method, thereby increasing the confidence in the data base. In order to bring attention to the biovolume index, I will only discuss this procedure here. The paleoecological interpretation of the faunal data used is presented elsewhere (Ausich 1979).

Initial reconnaissance of fossiliferous localities during a paleoecological study of Lower Mississippian (Edwardsville Formation) delta platform sediments indicated that crinoid stem debris and broken bryozoan colonies were numerically the most abundant faunal elements. Standard methodology entails counting the minimum number of individuals of each species in a given sample and excludes consideration of fragmentary faunal elements. This methodology was considered inadeqauate for this Mississippian study, and it is probably inadequate for many Paleozoic settings. In previous studies, taxa such as crinoid pluricolumnals, bryozoans, and algae were normally treated separately from other groups and were classified as being either abundant, common, or rare. Meaningful comparison between abundant-common-rare determinations and numerical counts of different taxa from the same sample cannot be made. Only in extremely rare instances where crinoids and bryozoans are

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preserved *in toto* can abundance counts be made on these taxa.

In this study taxonomic abundance is presented as a percentage of the volume of fossil material in a sample. In this way fragmentary colonial organisms (bryozoans and colonial corals) and crinoid pluricolumnals are compared in a meaningful way to the abundance of other taxa in a single sample, and these "problem taxa" are compared meaningfully between different samples.

The percent volume measure is equivalent to the biovolume index proposed by Walker (1972a, p. 85) and is the paleontological analog of biomass. Biomass is a function of the amount of energy expended by an organism to make soft tissue; whereas, skeletal biovolume is a function of the amount of energy expended to construct skeletal material. These two measures are not directly analogous, but they are two different means for determining relative energy budgets in communities.

The demographic techniques described here were used to evaluate three contemporaneous, laterally contiguous delta platform facies on the Lower Mississippian Borden deltaic complex (Ausich *et al* 1979, Ausich and Lane 1980). The facies examined include the following: submarine natural levee sandstone channels (Waldrip Site, IU 15107 and IU 15127), interdistributary mudstone facies (Boy Scout Camp, IU 15109), and a skeletal carbonate bank (Allens Creek bank, interbedded limestones and siltstones, IU 15113 to IU 15122) (IU, Indiana University locality numbers). All facies are situated in the Edwardsville Formation and are shoreline exposures along Monroe Reservoir, Monroe County, Indiana.

These facies contained a combination of complete, broken, and disarticulated skeletal material. The siltstones of Allens Creek bank and the interdistributary mudstones are easily disaggregated; and therefore, matrix-free fossil debris is readily obtainable. In contrast, fossils from the limestones of Allens Creek bank and the distributary sandstones are not easily isolated. Meaningful data must be obtained from surfaces or point counts from thin-sections.

METHODS

Procedure for Mudstones and Siltstones. Bulk samples of twenty ℓ each (eight 7x12 in sample bags of material) were collected from selected siltstones on Allens Creek bank and from the interdistributary mudstones. From each 20ℓ sample, one ℓ of material was separated using a 25x19 cm sample splitter and each sample was then processed and wet seived. Mudstone samples from the interdistributary mudstones were initially soaked in water and sieved, then boiled in water and soda ash (Na_2O) and resieved. Siltstones from Allens Creek bank were also initially soaked in water and sieved, then boiled in water and the detergent Quarternary-O before being resieved. Most siltstones from the bank contained more carbonate than did the mudstones, and Quarternary-O facilitated the disaggregation of these more indurated sediments.

The one ℓ portion isolated from each original sample was wet sieved through a sieve stack containing sieves with the following U.S. standard sieve mesh numbers: 5, 10, 20, 40, 60, 80, and 100. The remaining 19 ℓ of each sample was sieved through only the 5 mesh.

The limits of practicality imposed by fossil picking time necessitated that only certain fractions of the washed residues be examined for fossil content. In the sample fractions examined for fossils, every piece of fossil debris was identified as precisely as possible. In the 5-mesh residues, all the fossil residue was identified, but in smaller mesh sizes of the one ℓ sample only a fraction of the one ℓ residue was examined. These subsamples were obtained by sample division using a sample splitter. Therefore, in the mesh sizes smaller than five, a multiplication factor was used to convert each count or weight determination to that of a 20 ℓ equivalent. Although the examination of a subsample may introduce biases, this is the only practical procedure. The fraction of the 20 ℓ residue examined for each sieve size is given in table 1.

TABLE 1

Fraction of each sieve size picked for entire fossil content in bulk siltstone and mudstone samples.

Sieve Size (#)	Fraction of 20 ℓ sample
5	1/1
10	1/80
20	1/640
40	1/5120
60	1/5120
80	1/10240
100	1/10240

In order to compute the biovolumes, each taxon was weighed and multiplied by a weight-volume conversion factor. This conversion factor was calculated by determining the volume of a known weight

of crinoid stem debris from each sample. As an example, in sample IU 15109-9000 (unit 9 from the interdistributary mudstone facies) a 295 ml volume of crinoid stem debris weighed 784.8 gm, yielding a conversion factor of 0.38 ml/gm. The volume of a fossil species from this sample could be calculated by multiplying the weight of recovered debris of that species by 0.38. An assumption in this conversion is that all fossil material in each sample is preserved in a similar manner. This assumption was reasonable for the samples in my study but may not be appropriate in every situation.

For each species, the biovolume (and numeric counts) for 20 ℓ equivalents was determined for each sieve fraction, then all the biovolume determinations were pooled (see figure 1).

Abundance data obtained both by the biovolume method and by the standard method of counting the minimum number of individuals of each species in each sample are given. Abundance data are presented both ways so that the relative utility of each method can be compared and so that previous studies with count data can be compared to the data from the present investigation. Percent diversity is also given and is used as a measure of species richness. Percent diversity is calculated by dividing the number of species of a given taxon by the total number of species in the community.

Contiguous vertical samples (n=13) were evaluated from the 2.6 m section of interdistributary mudstone at the Boy Scout Camp (IU 15109), and 8 siltstones of Allens Creek bank were sampled. An attempt was made to identify all fossil debris to the species level. This was not possible for only a few crinoid stem fragments, and it was not attempted for macroinvertebrate debris in the 40 mesh and smaller fractions. In these instances, biovolume measurements for such samples were placed in categories such as miscellaneous crinoids or miscellaneous fenestrate bryozoans. In each sample where miscellaneous categories were present, the miscellaneous biovolume was distributed to each identified species in the appropriate higher taxon on a proportional basis to produce corrected biovolumes. The corrected biovolumes maximize the amount of biovolume that is placed in named taxa for each sample. I believe that this is the most accurate documentation of relative abundances. Abundance for each taxon can be presented as follows: absolute numerical abundance (percent numerical abundance); absolute biovolume abundance (percent biovolume abundance); and if appropriate, absolute corrected biovolume abundance (percent corrected biovolume abundance).

Procedure for Limestones and Sandstones. Percent area data was collected for the skeletal components on limestone and sandstone bedding surfaces. Theoretically, numbers derived from areal surveys on bedding surfaces can be multiplied by one (length unit) to yield a volumetric count; therefore, it can be assumed that percent area on bedding

		MINIMUM NUMBER OF INDIVIDUALS	WEIGHT (IN GMS.)	CONVERSION FACTOR TO ENTIRE SAMPLE	CORRECTED MINIMUM NUMBER OF INDIVIDUALS	CORRECTED WEIGHT	WEIGHT TO BIOVOLUME CONVERSION FACTOR	CORRECTED BIOVOLUME	% TOTAL BIOVOLUME ABUNDANCE (FOR SAMPLE)	% TOTAL NUMERICAL ABUNDANCE (FOR SAMPLE)
	80	-	-	10240	-	-				
	100			10240						
	TOTALS	-	-	-	2	0.2000	0.3759	0.0752	0.0036	0.0009
CLEIOTHYRIDINA PARVIROSTRA	5	22	3.8000	1	22	3.8000				
	10	2	0.0880	80	160	7.0400				
	20	2	0.0026	640	1280	1.6640				
	40	-	-	5120	-	-				
	60	-	-	5120	-	-				
	80	-	-	10240	-	-				
	100	-	-	10240	-	-				
	TOTALS	-	-	-	1462	12.5040	0.3759	4.7003	0.2238	0.6867
COMPOSITA GLOBOSA	5	19	5.2000	1	19	5.2000				
	10	3	0.0588	80	240	4.7040				

FIGURE 1. Example of biovolume data sheet completed for *Cleiothyridina parvirostra*. 5, 10, 20, *etc.*, represent sieve mesh sizes.

surfaces can be compared directly in a meaningful way with the percent volume data that were collected for the mudstone and siltstone samples. These data are all considered as biovolumes. Raw counts of fossils from limestones and sandstones were also made so that these data could be compared with percent area data.

1 m^2 grid was used to estimate the relative percentage of each taxon on bedding surfaces. Bedding surfaces were point counted using grid spacing of 5 cm drawn on a sheet of acetate. The grid was placed on bedding surfaces in the field, and the identifications of rock constituent or fossil under each grid intersection was made and recorded on magnetic tape with a portable cassette tape recorder. Four hundred identifications were made in each m^2.

On Allens Creek bank, a total of 24, 1 m^2 areas or 9600 identifications were made on bedding surfaces of a single outcrop (IU 15115). The categories considered in identification were crinoid fragments (crinoid columnals and pluricolumnals with a maximum exposed diameter greater than 5 mm), matrix (all fossil material under 5 mm and all non-fossil material), and identifiable fossil taxa.

On distributary sandstones, only slab IU 15127 was appropriate for an areal point count. The relative abundance of taxa at the Waldrip Site was computed using counts of the number of individuals of each species. This treatment was adequate at the Waldrip Site because of the extraordinary preservation of complete crinoids and bryozoans. In this study only at this one locality does the standard methodology accurately reflect the relative abundances of the fauna. Abundances for areal counts at the Waldrip Site and Allens Creek bank were presented as minimum number of individuals, biovolume, and corrected biovolume as outlined above.

DISCUSSION

Plots of percent biovolume, percent numeric abundance, and percent diversity are given in figure 2. Percent biovolume is the index which is considered most meaningful; whereas, percent numeric abundance is typically the index used for paleoecological studies. Only in one instance was percent biovolume and percent numeric abundance concordant within a sample (distributary sandstone channel community, fig. 2A). In the distributary channels, nearly all preserved organisms were whole, yielding comparable biovolumes and numeric abundances. Such preservation is rare in the fossil record.

All other facies examined contained a combination of complete and fragmentary material. When standard procedure for determining numeric abundance is used in these facies, the abundance of characteristically fragmentary organisms (especially bryozoans and crinoids) is commonly overlooked; whereas, the abundance of organisms that are characteristically preserved whole is greatly exaggerated (organisms such as brachiopods and especially small organisms such as foraminifera and ostracodes).

With the biovolume method, sample evaluation more closely approaches requirements of statistical randomness. Either every piece of fossil debris was considered in a sample or subsample of shale, or quadrant point counting on bedding surfaces was used. Within each sample statistical randomness should be assured, but I perceive no practical procedure for the selection of sample sites which would give absolute statistical randomness for the data. Sample selection will vary among studies depending upon factors such as the distribution and density of fossils, the distribution of lithologies, the scale of the study, *etc.* (See fig. 2, CD.)

All groups of fossils must be considered with equal rigor with the biovolume method. This is very important for the reconstruction of paleo-communities and is commonly not practiced. Presented as a percentage of the total biovolume, data is easily comparable between different samples from the same facies and also between samples from different lithologies and from different geological settings.

As a relative abundance index, biovolume has a distinct advantage over numerical abundance indices in that fragmentary and colonial organisms are treated in the same way as solitary and whole organisms. The assumption inherent in this biovolume index is that skeletal mass can be used as a means of determining relative energy budgets. Biovolume is not directly analogous to biomass. Biomass is a measure of the soft tissue standing crop; whereas, biovolume is a measure of the skeletal debris contribution to the sediment. Biases introduced into paleontological data such as time averaging and variable life spans are difficult to remove, and are an assumed part of the biovolume index. As defined herein,

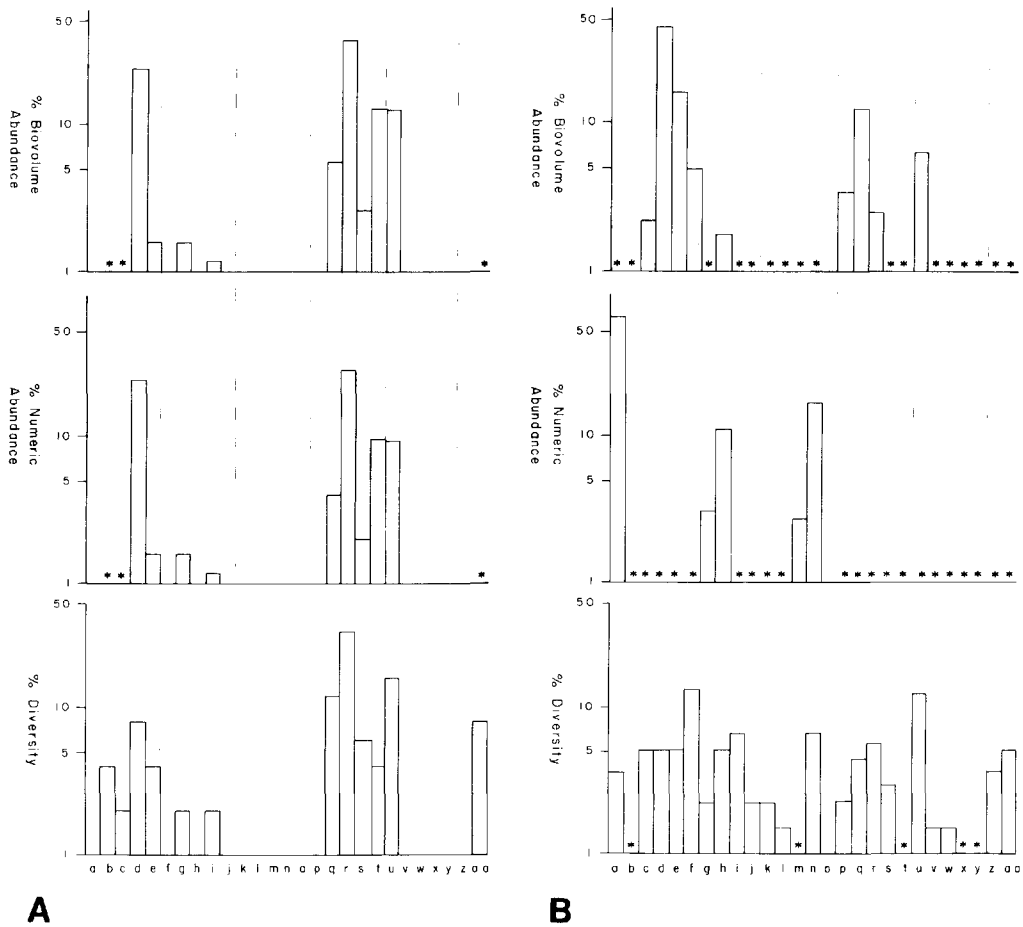

FIGURE 2A and B. Log histograms of % biovolume abundance, % numeric abundance, and % specific diversity of A, the total submarine natural levee community; B, interdistributary mudstone community. An asterisk (*) indicates taxa with abundance or diversity less than 1%. a=foraminifera; b=sponges; c=coelenterates; d=fenestrate bryozoans; e=cystoporate bryozoans; f=other bryozoans; g=strophomenid brachiopods; h=spiriferid brachiopods; i=other brachiopods; j=annelids; k=gastropods; l=bivalves; m=trilobites; n=ostracods; o=blastoids; p=disparid crinoids; q=cyathocrine crinoids; r=poteriocrine crinoids; s=flexible crinoids; t=diplobathrid crinoids; u=monobathrid crinoids; v=stelleroids; w=echinoids; x=holothurians; y=chordates; z=position uncertain; aa=trace fossils.

the biovolume measure is a measure of the amount of energy expended by organisms to construct skeletons that contribute to the rock record.

Other factors potentially limit my data. Only a 20 ℓ sample for large fossil debris and 1 ℓ sample for small fossils were analyzed for each sample, and only taxa represented by hard parts were treated. Organisms with different mineralogies must be treated separately, and epizoans cannot be dealt with. Inaccuracies in weight determinations may occur due to preservation by permineralization, but this problem was not a concern in my investigation.

Every paleontologist cannot be an expert in every group, and as a result, many studies have ignored certain components of the fauna, commonly bryozoans, crinoids, and algae. These groups were dominant in many Paleozoic epicontinental settings and should not be overlooked. A general examination of most invertebrate groups is usually sufficient for determination of the

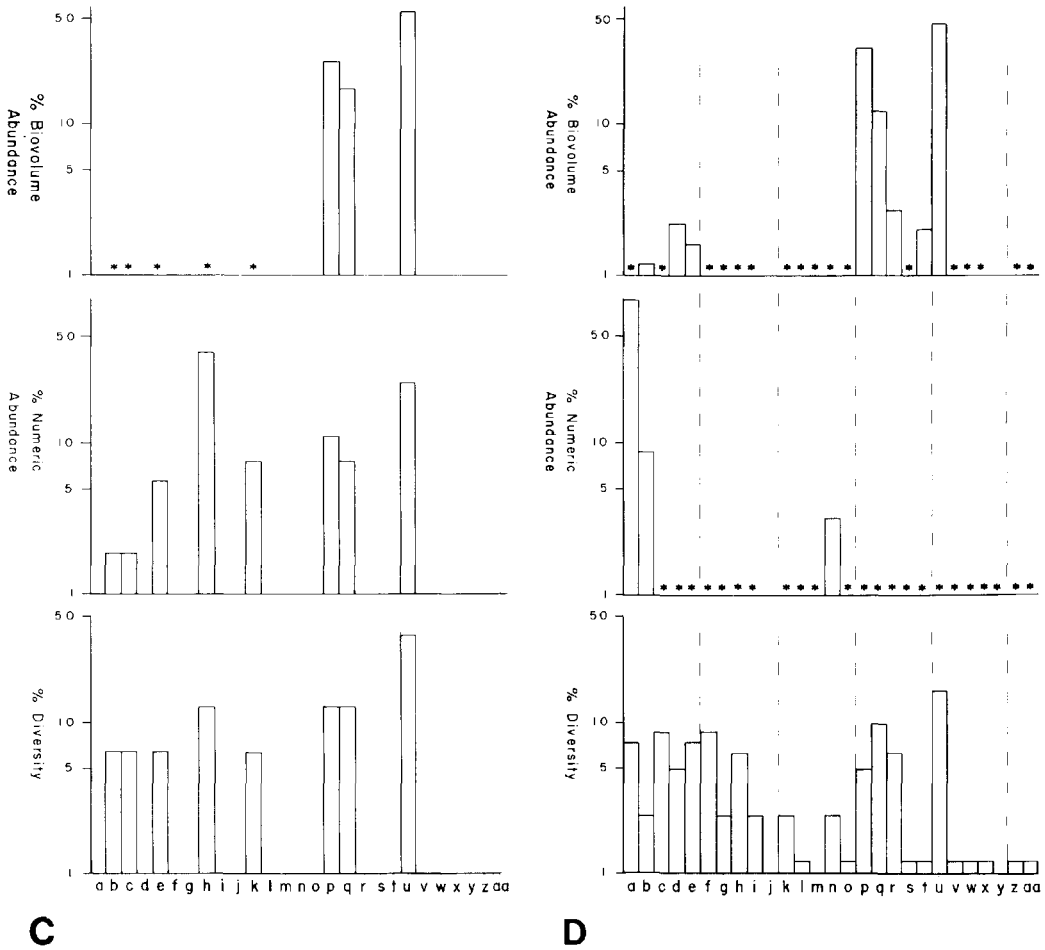

FIGURE 2C and D. Log histograms of % biovolume abundance, % numeric abundance, and % specific diversity of C, limestone bank community; and D, siltstone bank community. See figure 2A and B for description of code on taxa.

taxonomic groups (species) in a sample. A complete evaluation of a sample will allow the identification of different taxonomic groups, which should represent different paleoecological groups. The compromise of taxonomic identification is justified by the increased paleoecological information gathered by considering entire communities in the holistic approach (Kauffman and Scott 1976).

The biovolume index method discussed herein allows paleoecologists to approach more confidently studies with a holistic scope. The biovolume index described is a very useful paleoecological tool because it bypasses several problems inherent in census demography, and it is readily adaptable to a variety of sedimentological settings. This biovolume demography will improve sample fidelity (in the sense of Holtzman 1979, fig. 1) and will provide a firm data base for interpretation. Depending upon the sample and the philosophy of the investigator, biovolume diversity numbers can be used for paleoecological reconstruction, taphonomic analysis, or fossil assemblage fidelity.

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