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REPRODUCIBILITY OF BIOVOLUMETRIC PARAMETERS IN COMMUNITY RECONSTRUCTION[1]

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ABSTRACT. Criticisms have been raised about the inadequacies of methods in community paleoecological analysis. Until recently, most paleoecological studies were done by specialists in individual taxonomic groups. Because of this specialization, most data collected favored certain groups. Other fossils were either ignored, discounted, or loosely labelled qualitatively under descriptive terms as: rare, occasional or abundantly present.

Ausich (1981) and Boucot (1981) have independently proposed methods of community analysis whereby the biovolume (shelly biomass) of all taxa present are quantified. To date, little has been done to substantiate the reproducibility of data obtained in this manner for level, soft-bottom, Paleozoic communities. A level, soft-bottom, Middle Devonian community is analyzed here using the sampling model proposed by Ausich (1981). Trends in the comparisons of biovolume to minimum number counts are shown to be reproducible as are trends in each of these catagories within individual horizontally continuous beds. Informational loss and quantitative reproducibility for this new method is shown to be an improvement over prior methodology.

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INTRODUCTION

The manipulation of data in paleoecological studies has become increasingly sophisticated in recent years. Cluster analysis, factor analysis and canonical variate analysis are but a few of the techniques that have become commonplace in paleoecological studies (Raup and Stanley 1978). A concern for the reliability of the data on which these analyses are performed has been raised (Ausich 1981). Limitations on the standard method using minimum number counts of individuals within each taxon have been discussed for some time, but little has been done to improve the situation. Fragmentary faunal elements in minimum number counts representing evidence of sponges, holothurians, crinoids, blastoids, many bryozoans and other fossils that disarticulate are difficult to evaluate. Relative importance of these individuals within the community is largely masked. Efforts to understand the relative importance of community constituents by inclusion of ordinal ranks like abundant,

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common or rare (Broadhead 1976) are subjective and cannot be used in direct comparisons with quantitative data.

In 1981, Ausich proposed a new method for the collection of data for community reconstructions based on biovolume. Boucot (1981) independently suggested a similar idea termed "shelly biomass." These concepts are derived from ideas presented by Walker (1972) on trophic analysis: "The percent volume measure is equivalent to the biovolume index proposed by Walker and is the paleontological analogue 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" (Ausich 1981). There is no meaningful relationship between the 2 terms, yet each is a quantitative measurement of relative energy budgets in communities.

In his study, Ausich bulk-sampled equal volumes of 3 contiguous Mississippian age delta complex facies in Indiana and wet-sieved the samples to collect all possible biotic components. Both biovolumetric and the commonly used numerical counts (Feldman 1980) for each species were made from the sieved fractions. The method being tested here is that of determining percent biovolume. Comparisons of 2 tables, biovolumetric abundance and numerical abundance, ought to illuminate trends in their similarities and differences. In the Ausich study, only once were the 2 parameters of percent biovolume and percent numerical abundance concordant. It was noted that this may be expected only if nearly all the fossils were preserved whole. Preservation of only whole skeletons is rare, indeed, in the fossil record.

Limitations in obtaining reproducible biovolumetric data have been discussed earlier (Ausich 1981), but most objections to the use of biovolumetric measurements center on 3 problems: (1) contamination of fossils by uncleanable matrix, (2) whole speciments with matrix-filled body cavities and, (3) unidentifiable fragments. To disregard these problems could invalidate the purpose of the measurements themselves: that of reproducible quantitative data. These problems are encountered in nearly every reconstruction but are not insurmountable in themselves and do not automatically rule out the use of biovolumetric measurements. Matrix can, in many cases, be mechanically or chemically removed, providing the shelly material is not lost in the process. In instances where large numbers of specimens are available, clean conspecific individuals of like size and shape can be inserted as replacements for those that are problematic. The same holds true where whole specimens with matrix-filled body cavities are found. If needed, substitution by 2 single valves of correct size, shape and taxon can be made. Seldom are fragments so poorly preserved or so fragmented that they cannot be identified to the class level and, in most cases, to the generic level. These fragments can then be divided proportionally into the lower levels of the taxonomic group to which they belong. In this manner the biovolumetric measurements take into account all possible evidence of biota within the samples.

METHODS

To test the reproducibility of data collected in accordance with the biovolume method, data collected from bulk-sampling of multiple sites within 5 shale horizons of the Middle Devonian (Givetian) Silica Shale were compared. These horizons were highly fossiliferous and exposed in readily accessable quarry high walls in north-eastern Indiana, near Ft. Wayne (fig. 1). Two vertical columns, 20 m apart laterally, labeled "North" and "South" in fig. 2, were bulk-sampled, prepared, and the contained specimens were counted. The depositional environment of the sampled units was that of a level, soft-bottom delta shelf. Wiedman (in press) showed the community at this locality to be dominated by articulate brachiopods, but it also included 41-55 genera of other macrofossils. The community included 13 genera of articulate and 3 genera of inarticulate brachiopods, 4 tabulate and 5 rugose corals, 8 mollusks, 3 trilobites, 5 crinoids, 2 blastoids, and 12 bryozoans. Bulk-sampling and specimen-preparation procedures duplicated techniques of Ausich. This included wet-sieving

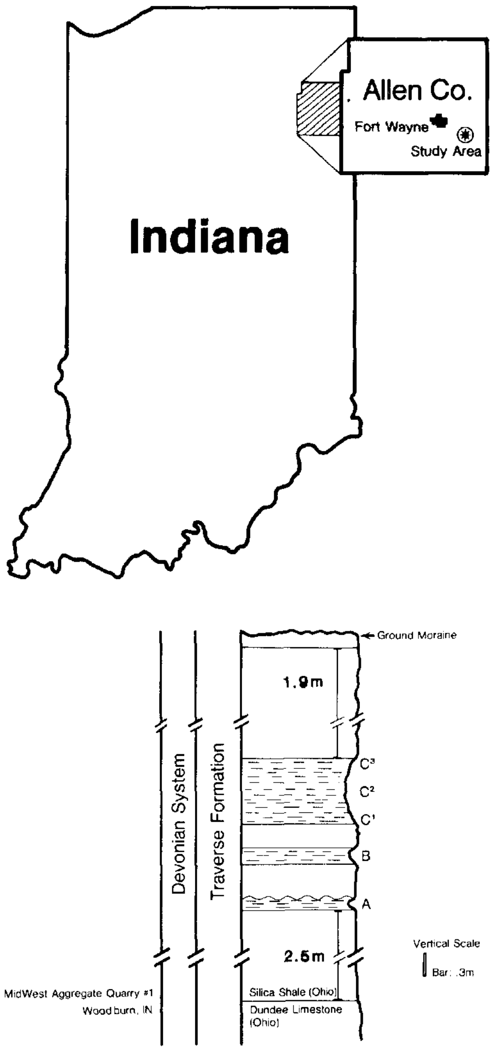

FIGURE 1. Portion of stratigraphic column sampled in study with study area location for the Midwest Aggregate Quarry No. 1.

through a standard sieve stack including 5, 10, 20, 40, 60, 80 and 100 size ranges. More than 7,000 specimens were recovered. The large number of specimens allowed for liberal, yet reliable, substitution if individuals were problematic.

RESULTS AND DISCUSSION

Biovolumetric information accumulated by Ausich (1981) was believed reproducible with much greater certainty than the more commonly used percent numerical abundances. However, time limitations did not allow for this supposition to be tested. Data from the northeastern Indiana Devonian study, used here, substantiated the reproducible nature of the biovolumetric parameters. In each sampled bed, the percent biovolumetric abundance remained relatively constant within that bed, whereas the traditionally computed percent numerical abundance was commonly erratic (fig. 2). Within individual units, the reasons for any discordant nature of the plots could commonly be determined. The most readily seen disparity is evident in one horizon, (labeled C_2, fig. 2), where an unusually large number of whole juvenile brachiopods of the genus *Strophodonta* was found at one sample site. Adult *Strophodonta* specimens are normally large at this site with dimensions of 7 × .5 × 2 cm being quite common. The juveniles collected were of uniform size with average dimensions of 1 × 1 × 0.2 cm. Obviously, in a sample with total sample size of a few hundred specimens, a disproportionate juvenile population of over 100 specimens from one species will skew the numerical abundance results. Without additional information, such as biovolumetric measurements can provide, one could be led to believe that this community was strongly dominated by *Strophodonta* brachiopods when, in fact, this is probably not the case. Inspection of the percent biovolumetric abundance graph (fig. 2) indicates that the dominance of *Strophodonta* does not manifest itself. The entire sample of juveniles collectively equals less than the biovolume of one average adult and thus becomes of little importance in the biovolumetric consideration. Not only is the reproducibility of biovolume helpful, but it also aids in representing a truer picture of importance within the community. In this case, the several juveniles probably had about the same effect on the community's limits of space and food as one adult.

The time-averaging effects of the fossil record are apparent to all who study paleoecology. Because of this time averaging,

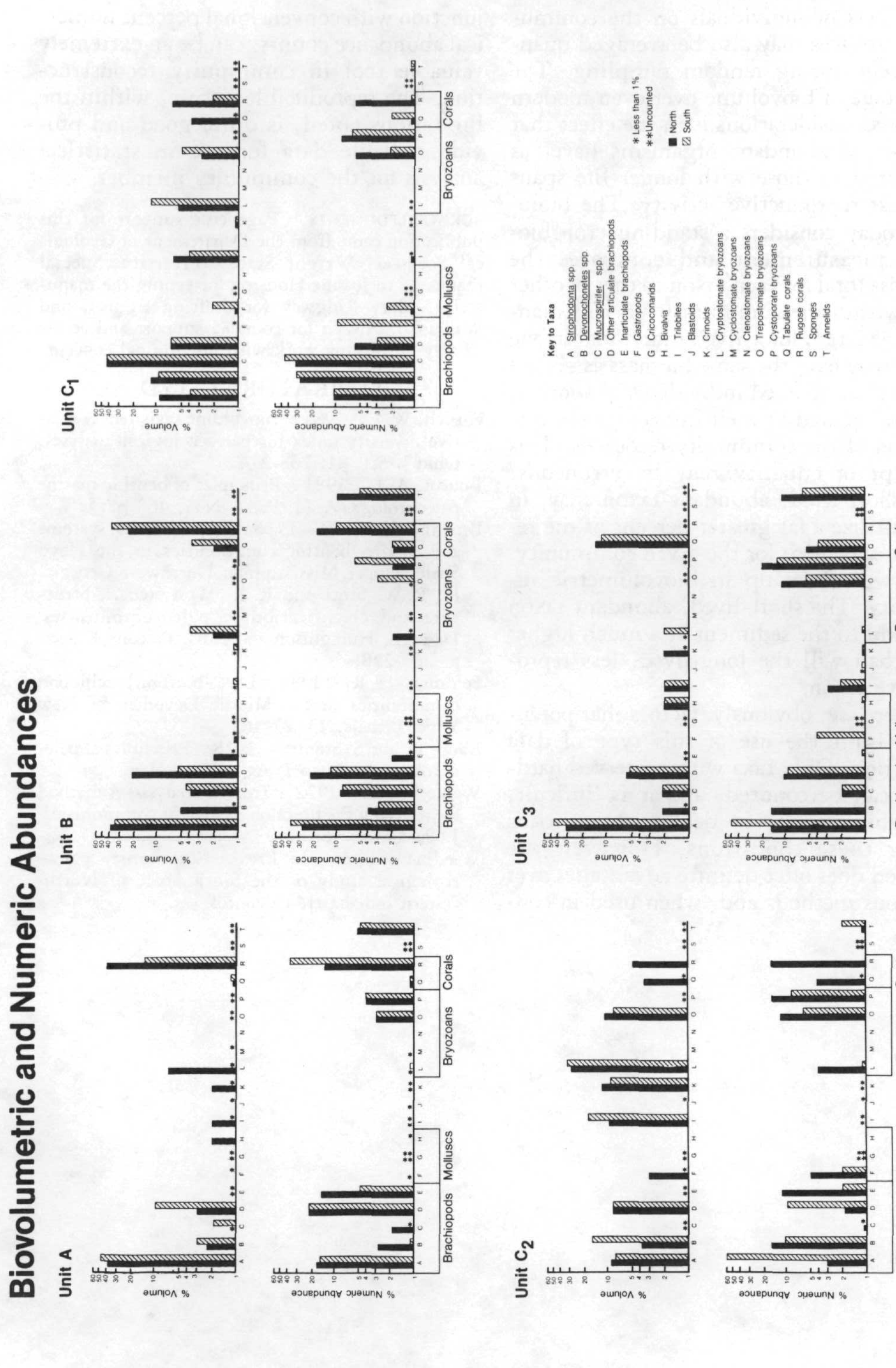

FIGURE 2. Biovolumetric and numeric abundances, plotted logarithmically by stratigraphic units sampled, with the North and South columns adjacent to each other.

the effects of individuals on the community resources may also be averaged quantitatively during random sampling. The advantage of biovolume over even modern biomass considerations is in the effect that short-lived abundant organisms have, as compared to those with longer life spans and less reproductive activity. The biologist today considers a standing crop biomass measurement and compares the biomass total for each taxon to that of other taxa within the community. In this manner, one large, long-lived individual in one taxon may have the same biomass as several smaller, short-lived individuals of another, and be equated to their impact on the utilization of the community resources. This concept of equality may be erroneous. The short-lived, abundant taxon may, in fact, utilize a far greater percent of the resource allotment for the given community. This will show up in biovolumetric inequality. The short-lived, abundant taxon will add to the sediment at a much higher rate than will the long-lived, less reproductive taxon.

There are, obviously, factors that potentially limit the use of this type of data collection. Only taxa with preserved hardparts can be counted, and it is difficult, though possible, to deal with epizoans under these conditions. However, the method does offer definite advantages over previous methods and, when used in conjunction with conventional percent numerical abundance counts, can be an extremely valuable tool in community reconstruction. The reproducible nature, within the limitations noted, is quite good and provides reliable data for use in statistical analysis for the community member.

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