



FORAMS 2006

## **Micro- to Macro-scale Foraminiferal Distributions: The Contributions of Martin A. Buzas**

Stephen J. Culver

*Department of Geology, East Carolina University, Greenville, NC 27858, U.S.A.  
culvers@ecu.edu*

Received: 22/05/2006 Accepted: 15/07/2006

### **Abstract**

The research that Martin A. Buzas has published over the past more than 40 years has influenced us greatly. That research has many strands that cannot be dealt with in this short review. However, the theme of micro- to macroscale foraminiferal distributions is interwoven throughout Buzas's research career. Distributions are something that Buzas is very fond of. He was trained in statistics as well as foraminifera and so it was inevitable that he would combine his knowledge of statistical distributions with foraminiferal distributions at several different scales. He has studied the distribution of foraminifera at microscales, horizontally within a 10 cm<sup>2</sup> area of the sea floor or vertically, cm by cm within a 20 cm core. He has also worked at the mesoscale, quantifying, through the pioneering use of the General Linear Model, the relationship of foraminiferal distributions and environmental variables in space and time. This research led to the hypothesis of pulsating patches. He has worked at the macroscale with S. J. Culver, defining the distribution of benthic foraminiferal provinces, showing that all foraminiferal distributions, particularly around the coasts of North and Central America, belong to the same statistical distribution. Their work has documented the assembly and disassembly of communities and the latitudinal patterns of deep-sea benthic foraminiferal diversity in the Atlantic basin. Most recently, with his coauthor, mathematical statistician L. C. Hayek, Buzas has delved deep into the intricacies of species diversity and solved a 50 year-old supposedly intractable problem of mathematically relating species richness with species evenness. This work led to the introduction of new approaches to understanding community structure and recognizing boundaries between adjacent communities (SHE analysis). Many of us work long hours and publish many papers over our careers but few of us truly influence the fundamentals of our science. Marty Buzas is one micropaleontologist whose work will be of lasting significance.

**Keywords:** Foraminifera; distributions; Martin Buzas.

## 1 Introduction

A 42-year (and still counting) research career that has dealt with many ecological and micropaleontological topics and that has resulted in over 100 publications is difficult to summarize. However, the theme of distributions runs throughout the career of Martin A. Buzas. Buzas is unusual in that he was educated (or, rather, he educated himself) in statistics as well as foraminifera. Thus, he has been able to use his knowledge of statistical distributions to illuminate his work on foraminiferal distributions. Buzas also pioneered the use of multivariate numerical and statistical approaches to analyzing foraminiferal data. Many of the techniques that he has used have later been adopted by paleontological colleagues working on other groups of micro- or macrofossils. Given that he also received a formal education in ecology, Buzas has been able to straddle the divide between paleontology and ecology. Indeed, many of his publications are in ecological journals.

As an outgrowth to a session on foraminiferal distributions held at the FORAMS 2006 international conference held at Natal, Brazil, in September 2006, this paper attempts to summarize succinctly Buzas's contributions to this field. Given the breadth and depth of Buzas's work, this paper deals with foraminiferal distributions at three scales, micro-, meso- and macro-. Only the more important papers are referred to but it should be noted that the choice of publications is subjective and other researchers (including Buzas himself) might well choose others. Nevertheless, whichever papers are chosen, the fundamental contributions of Buzas to our science are indisputable. These contributions were recognized by the Paleontological Society when, in 2004, they honored him with their highest award, the Paleontological Society Medal.

## 2 Micro-Scale Distributions

Early in his career, Buzas described the spatial distribution and varying densities of benthic foraminifera in a 1 sq. ft. (ca 900 cm<sup>2</sup>) area in Rehoboth Bay, Delaware (Buzas, 1968). (He later pioneered studies of micro-distributions downcore; Buzas, 1974; 1977, Buzas *et al.*, 1993) The purpose of the study was, "...simply to find out what the spatial distribution of species is in an area where homogeneity of environmental variables might be expected" (Buzas, 1968, p. 1). Its importance lay in the fact that such knowledge is necessary for an understanding of spatial competition, reproductive-social behavior, and niche and, indeed, an understanding of how representative a single sample is, whether it be collected for ecological, paleoenvironmental or biostratigraphic reasons. Buzas designed a sampler that collected 2 ml samples in 36 contiguous cells

and took three replicate sets of samples at a muddy, shallow (<1 m) site. In the living population, 50% of cases for four species exhibited a random distribution. In the dead assemblage, 80% of cases for five species showed a random distribution. Those cases that were not random exhibited an aggregated distribution that Buzas explained as the result of asexual reproduction. Random distributions of rarer species were explained as the result of individuals settling out of the water column. The paper concluded with a two prescient sentences given the later debate concerning the relative value of live, dead and total assemblages (Scott & Medioli, 1980; Murray, 2000) and the paper (discussed below) where Buzas introduced his “pulsating patch” model for foraminiferal densities (Buzas *et al.*, 2002). “The observations presented here are like a single frame from a motion picture. Detailed observations over a period of time are required if one would gain an understanding of the true dynamic aspect of the populations” (Buzas, 1968, p. 11).

Variations in foraminiferal species densities and the explanation for them, in terms of environmental variables, were the subject of Buzas (1969a). In this paper, Buzas introduced an *a priori* general linear model to test hypotheses for differences in species densities, periodicity between stations, and relationships between species densities and environmental variables. Three stations in an estuarine tributary of Chesapeake Bay, Maryland were sampled monthly for 12 months for foraminiferal densities (three species) and several environmental variables (temperature, salinity, oxygen, chlorophyll a, b and c). The analysis demonstrated the very important fact that densities were explained by the entire set of variables. No one variable was significant individually. Furthermore, all three species exhibited periodicity but for each species the periodicity was different at the three stations. This paper was published at the time when foraminiferal distributions (including depth zonations) were generally explained by temperature and salinity, although it was becoming recognized that other variables likely played a role. Buzas (1969a) demonstrated this fact conclusively but were explanations tested in temperate regions applicable to tropical zones?

To address this question, Buzas repeated his 1969 temperate study in a *Thalassia* habitat in Discovery Bay, Jamaica (Buzas *et al.*, 1977). He sampled live foraminifera at two sites for 12 months. At the same time, water temperature, sediment temperature, salinity, oxygen saturation, water pH, sediment pH, sediment median, sediment sorting, turbidity, particulate organic carbon, *Thalassia* weight, and weight percent silt plus clay were measured. Again using a general linear model, Buzas *et al.* (1977) showed that, this time, patterns of species’ densities were not explained by the measured environmental variables. They concluded that abiotic variables do not regulate foraminiferal densities in the generally more benign (than temperate Chesapeake Bay), low

latitude Discovery Bay and that biotic factors such as competition and predation must be invoked. In particular, cropping by nondiscriminate predators was singled out as a likely important control on foraminiferal densities. This hypothesis was later tested by Buzas in several innovative caging experiments in the Indian River Lagoon, and on the shelf off Florida. Predation did indeed prove to be of great importance (Buzas, 1978, 1982; Buzas & Carle, 1979; Buzas *et al.*, 1989).

The results from the Florida experiments were so intriguing that Buzas collected replicate samples from the same site in the Indian River Lagoon for the 20-year period from 1977 to 1996. Buzas *et al.* (2002) pointed out that there had generally been a tacit assumption that seasonal periodicities of densities established over one year would apply to other years (*e.g.*, Buzas, 1965). Buzas & Severin (1993) demonstrated that this was not in fact the case in the Indian River Lagoon and Murray & Alve (2000) demonstrated density differences between years and seasons in a temperate intertidal zone. The value of replicate sampling was demonstrated by Buzas & Hayek (2000) who, in a four year study in the Indian River Lagoon, showed significant differences in foraminiferal densities among years, seasons and their interactions. Not only did densities differ among years and with seasons, but they differed differently with the seasons in different years. As Buzas *et al.* (2002, p. 68) explained, "In other words, every possible variation occurs." However, analysis of foraminiferal densities in the Indian River Lagoon over the entire 20 year sampling period (Buzas & Hayek, 2000) shows significant differences among years but no trend of increasing or decreasing densities. Indeed, there is a long-term equilibrium. To investigate this phenomenon in the Indian River Lagoon, Buzas *et al.* (2002) took monthly measurements of densities of five taxa along with seven environmental variables, with four replicates at each of three stations, over a period of five years. Analyses with general linear models showed that differences among stations, years, seasons and their interactions were all significant. Environmental variables contributed little to explaining density variations. Buzas *et al.* (2002) explained their data and analysis with a model of asynchronous or aperiodic pulsating patches. Their concise explanation cannot be improved upon. "We propose a model wherein individual foraminifers are spatially distributed as a heterogeneous continuum forming patches with different densities that are only meters apart; reproduction is asynchronous causing pulsating patches that vary in space and time. Thus we would expect significant differences among stations, years, seasons and their interaction. At the same time, no long-term increase or decrease in density for any of the taxa is observed. Evidently, long-term stability is achieved through considerable short-term variability in space and time. Although observations at a single station are not indicative of a larger area at any particular time, the concept of pulsating patches indicates that observations at a station will in the long-term give an assessment of a larger area" (Buzas *et al.*, 2002, p. 68).

### 3 Meso-Scale Distributions

Although Buzas pioneered the use of multivariate numerical and statistical approaches to the recognition of biofacies (*e.g.*, Buzas, 1967, 1969b, 1972; Mello & Buzas, 1968), his work on species diversity and related matters is emphasized here due to space constraints. We will see below, however, that recognition of biofacies and studies of species diversity are not mutually exclusive endeavors.

Species diversity of benthic foraminifera in the western North Atlantic was treated by Buzas & Gibson (1969). In addition to demonstrating a generally offshore increase in species diversity from inner shelf to abyssal depths, this paper used frequencies of species as well as the number of species. Thus, the distinction between species richness (S) and species diversity (the information function,  $H(S)$ ) was made for foraminifera for the first time. The paper also introduced E as a measure of species equitability or evenness. When species in a sample have identical proportions they are perfectly equally distributed and E (the ratio of  $E^{H(S)}/S$ ) is 1. This measure has been used extensively over the past almost 40 years to help interpret species diversity (H), including Gibson and Buzas's comparison of Miocene with modern patterns of species diversity in the western North Atlantic (Gibson & Buzas, 1973). However, the relationship between H, S and E was unclear. In other words, what were the relative contributions of S and E to any given value of H? Some workers stated, in print, that this problem was intractable but Buzas & Hayek (1996) demonstrated that  $H = \ln S + \ln E$  and solved that simple equation. This decomposition equation for the relationship of S, H and E (Buzas & Hayek, 1996) led Buzas & Hayek (1998) to use patterns of biodiversity (multispecies population structure), appropriately termed SHE analysis, to recognize biofacies.

The usual approach to defining biofacies quantitatively is to order all the possible similarities between stations along a gradient. A myriad of analytical techniques has been employed (cluster, principal components, factor, canonical variate, canonical correspondence, etc). SHE analysis for biofacies identification (SHEBI) utilizes a novel approach. Recognizing that biofacies, no matter how they are defined, do not all contain the same number of species, Buzas & Hayek (1998) accumulated data from contiguous stations such that S, H and E are examined as a function of the number of individuals (N). Because the expected behavior of S, H and E are known through the decomposition equation, departures from known expected outcomes define biofacies boundaries. When biofacies are identified, their component stations are serially deleted as the accumulation procedure is repeated. Because SHEBI analysis involves all components of species diversity, by examining the structure of multispecies populations along a gradient, it identifies biological community change.

Most recently, Buzas & Hayek (2005) summarized their thoughts regarding S, H and E. In pointing out the great interest in quantitative measurement of species diversity, they noted the contradictory published statements on the behavior of the components (S, H and E) of species diversity. They considered that confusion was due to whether or not sampling is carried out within or between communities and whether the statistical distribution underlying a biological community is determined. Further, they stated that the statistical distribution of  $p$ , the relative abundances from a community, must be known and the role of unequal, equal-sized, or accumulated samples must be appraised. Buzas & Hayek (2005) concluded by proposing and justifying the use of the log-series distribution as a null model for the determination of community structure.

#### **4 Macro-Scale Distributions**

Macro-scale distribution studies, of necessity, are based on large datasets which are very time-consuming to construct. Buzas moved into this area of study in 1978 when he began his collaboration with the author of this paper. Culver & Buzas (1980, 1981a, 1982, 1985, 1986, 1987) first documented the distribution of all species of benthic foraminifera that had ever been recorded along the Atlantic and Pacific coasts of North and Central America, in the Gulf of Mexico and in the Caribbean. Arctic data remain unpublished. Through multivariate analysis of taxonomically standardized data, they recognized latitudinally-related provinces on the shelf, much as others had done for various groups of invertebrates. However, the benthic foraminiferal data extended offshore beyond the shelf and foraminiferal assemblages at slope and abyssal depths differed more from shelf assemblages than northern shelf assemblages did from southern ones. Thus, the definition and distribution of provinces was extended across the entire continental margin and provincial boundaries were noted to occur at the boundaries between adjacent water masses (Buzas & Culver, 1980; 1990; Culver & Buzas, 1981b, 1981c, 1983).

Realm-scale values of species diversity (in this case, Fisher's alpha) were calculated for the continental margins of North and Central America (Buzas & Culver, 1991, 1999) and were found to follow the "classic" pattern of higher diversity in low latitudes and lower diversity in high latitudes. The highest value of alpha occurred in the Caribbean followed in descending order by the Atlantic, Pacific, Gulf of Mexico and Arctic continental margins. In each region, the distribution of species richness and occurrences conformed to the log series (Buzas & Culver, 1999). Differences in species richness among areas were explained by species occurring rarely and mainly by species

occurring just once or twice (87% of the difference in species richness between the Atlantic and Caribbean regions was accounted for by species occurring once or twice). Most of these rarely occurring species had no fossil record and were endemic to a particular region. The two regions of highest diversity (the Caribbean and Pacific) had the greatest number of endemic species (Buzas & Culver, 1991). Most of the rarely occurring, endemic species were considered to have evolved recently, indicating more origination in species-rich regions (Buzas & Culver, 1999). In summary, "All regions exhibit the log series distribution, have nearly equal proportions for abundant species, and differ only in the number of rare species that coexist. Thus, from the point of view of the distribution of occurrences, the most striking aspect is the similarity among regions (Buzas & Culver, 1999).

Buzas & Culver realized that this huge modern dataset was the key to understanding distributional patterns of benthic foraminifera in the Cenozoic fossil record. A subset (the Atlantic continental margin) was chosen and the worldwide stratigraphic ranges (partial species durations) of over 800 species was documented. In addition to extensive taxonomic standardization, lithologic information was standardized to current chronostratigraphic placement. Various paleobiological questions could then be addressed. The geographic distributions of first occurrences did not support the concept of centers of origin; originations occurred throughout the world oceans (Buzas & Culver, 1986; 1989). However, originations apparently increased in high latitudes during the late Cenozoic global cooling. Species duration data supported this trend. Species restricted to higher latitudes on the North American Atlantic shelf had average species durations of 7 million years, whereas species south of Cape Hatteras had average species durations of 20 million years. Thus, Buzas & Culver (1984) concluded that higher evolutionary rates characterized higher latitudes during the late Cenozoic. From study of species durations, they also found that evolutionary patterns and rates were the same for both rarely and abundantly occurring species and that rapid dispersal after origination was necessary to achieve species longevity (see Culver & Buzas, 1998, for further discussion and explanation of these patterns).

Analysis of the Atlantic shelf fossil dataset provoked some questions concerning community dynamics through the Cenozoic. To address these questions a large dataset was constructed for the portion of the central Atlantic shelf, the Salisbury-Albemarle embayment of Virginia and North Carolina. Foraminiferal census data from six Cenozoic formations, ranging from the lower Eocene to the upper Pliocene, were taxonomically standardized and full species durations for 356 species were recorded from the literature. Immigrations,

emigrations, originations and true extinctions all contributed to community dynamics over the last 55 million years of transgressions into and regressions from the Salisbury-Albemarle embayment (Buzas & Culver, 1994). During transgressions, communities were composed of a dynamic mixture of newly originated species and immigrants. During regressions, the species comprising communities either emigrated or became extinct (Buzas & Culver, 1994; 1998). When a new transgression returned inner shelf conditions to the embayment, new species originated and some of the previous emigrants returned as immigrants but many did not. Immigrant species were drawn from a species pool (the neritic species of the Atlantic and Gulf of Mexico continental margins). The composition of the pool continuously changed as new species originated and other species became extinct. This dynamic system was characterized by both faunal stability within ecological units and rapid and continual change. Balance and imbalance of immigrants versus emigrants was also observed (Buzas & Culver, 1998). Species behaved individualistically and there appeared to be no local community unity. Thus, no recourse to biotic interactions was necessary to explain observations. Rather, environmental regime was important in affecting community composition. In summary, "...the detailed composition of...assemblages is a result of the complex interplay of origination, extinction and dispersal characteristics of individual species, changing environmental conditions, and the recruitment (randomly or otherwise) from a species pool, where recruitment is to a considerable degree dependant on frequency of occurrence (Culver & Buzas, 1998, p. 221).

The Cenozoic Salisbury-Albemarle embayment time-slice data set proved ideal to investigate the relationship between species distribution, abundance, and occurrence and species duration for benthic foraminifera (Buzas & Culver, 2001). This relationship has great relevance to evolutionary studies. A significant positive relationship between both abundance and geographic range of species (*e.g.*, Rosenzweig, 1995) and abundance and frequency of occurrence (Hayek & Buzas, 1997) is well established. Because species with wide geographic ranges are more likely to survive localized environmental catastrophes than those geographically restricted to the disaster area, a positive relationship between geographic range and species duration is logically expected. Indeed, such a relationship is widely accepted as established fact (Rosenzweig, 1995). Analysis of the foraminiferal data confirmed a positive statistical relationship between geographic range, abundance and frequency of occurrence. However, unexpectedly, regression of species durations against frequency of occurrences for each time-slice, as well as regressions of durations against abundance of individuals in each time slice, indicated almost no relationship.

Buzas & Culver (2001) explained this conundrum in the context of the small size and extreme fecundity of benthic foraminifera. Even "rare" species,



represented by one or two specimens in a few cm<sup>2</sup> sediment sample, when scaled up to a few km<sup>2</sup> of seafloor, represent populations of many millions of individuals. Thus, species with few occurrences, although geographically restricted, have vast numbers of specimens, which mitigates against extinction. Buzas & Culver (2001) concluded that, following origination of a species, a two or three million year “trial period of establishment” takes place. In contrast to most other studies (of larger invertebrates), the likelihood of extinction of species that survive the initial trial period is the same, regardless of their distribution-abundance-occurrence characteristics.

## 5 Conclusions

The research of Martin A. Buzas is unusual in several ways. It involves ecological as well as paleontological insight. It involves massive data sets, even when small-scale problems are being addressed. It involves rigorous statistical analysis. But perhaps the most significant characteristic of this research is the imagination that allows interesting and significant ecological, paleoecological, biological and paleobiological questions to be formulated and then appropriately addressed. Over the years there have been many of these imaginative moments. But what comes through Buzas’s body of research is the pattern to this thought. As can be seen from this review, a scientific question is addressed but the result inevitably leads to another question which, in turn, is then addressed. For each of the three scales of distribution study discussed herein, a line of enquiry initiated 30 or 40 years ago is still active today. Many of us publish a considerable number of papers during our careers but few of us make the lasting impact that the research contributions of Marty Buzas have surely made.

## 6 Acknowledgement

I thank Marty.

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