

Ecological, Evolutionary, and Taphonomic Comparisons of Brachiopods and Bivalves at Multiple Spatial and Temporal Scales

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Abstract

The fossil record is the primary source of information on the history of life. As such, it is important to understand the limitations of this record. One critical area in which there is still much work to be done is in understanding how the fossil record, and our interpretation of it, may be biased.

Herein, the fidelity between the life and death assemblage of an extant brachiopod with respect to morphological variability is studied using geometric morphometrics. The results from several analyses confirm a high degree of morphological variability with little change in mean shape between the living and sub-fossil assemblage. Additionally, there is no evidence of distinct morphogroups in either assemblage. These trends persist at all depths and size classes indicating that this species could be recognized as a single, rather than multiple, species if only fossil data were available.

The second chapter involves the recognition and quantification of a worker bias in monographs of brachiopods and bivalves. Most specimens studied came from the 65th to 69th percentile of their species' bulk-collected size-frequency distribution. This indicates a significant bias toward monograph specimens that are larger than the mean size of the bulk sample. When compared at the species level, this bias was found to be highly consistent among the 86 species included in the study. Thus, size measurements of monographed specimens reliably and consistently record a similar size class for any given species, and this bias is easily corrected during meta-analyses.

Chapter three focuses on bivalves and brachiopods from a modern tropical shelf and quantifies the magnitude of time averaging (temporal mixing) for these two different organisms. This is accomplished by dating a suite of shells from each site using amino acid racemization calibrated with several radiocarbon dates. By studying the age distributions for each species it is determined that, despite some site to site differences, both bivalve and brachiopod species exhibit a similar time averaging magnitude when collected from the same region or depositional system. This indicates that fossil assemblages of these species may have very similar resolution.

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INTRODUCTION AND OVERVIEW OF THE RESEARCH

As one of the primary sources of information on the history of life, the fossil record is an important resource for anyone trying to understand the patterns and processes of evolution. During the past several centuries, intensive study of the fossil record has led to many important breakthroughs that have greatly increased our knowledge of how life on earth began and how it has prospered. Despite these insights, there is still much that we do not know.

One critical area in which there is still much work to be done is in understanding how the fossil record may be biased. Biases in the fossil record can take many forms, and the study of most of these biases can be grouped under the heading of Taphonomy. Taphonomy is literally the science of the “laws of burial” (from the Greek *taphos* + *nomos*), and was practiced long before the term was first coined by Efremov (1940). In fact, some of the first taphonomic investigations were conducted by Leonardo da Vinci, who used observations on living and dead bivalves to infer that fossils found in nearby mountains had not been transported there by the Biblical Deluge, but rather had lived and died *in situ* (Martin 1999). As the science of taphonomy has emerged as a distinct entity over the last two decades, its principles have been applied rather broadly to the fossil record, and its definition has solidified as “the study of the processes of preservation and how they affect information in the fossil record” (Behrensmeier and Kidwell 1985). Some general principles of taphonomy that have been outlined by Wilson (1988), and modified by Martin (1999) are as follows:

1. Organisms are more likely to be preserved if they have hardparts.
2. Preservation is greatly enhanced by rapid burial, especially in fine-grained sediment and/or in the absence of decay and scavenging. Rapidly buried deposits can serve as ecological “snapshots” of the living community.
3. During the transition from a living assemblage of organisms to an assemblage of the remains of dead organisms, disarticulation and chemical alteration resulting from decay, abrasion, transpiration, predation, scavenging, or dissolution can cause the loss of information about species abundances and community diversity and structure. This information loss is typically most severe in shallow-water marine depositional systems.
4. Fossil assemblages typically consist of spatially-averaged remains. That is, a fossil assemblage can consist of organisms that have been preserved in life position, organisms that have been disarticulated, reoriented, or concentrated from the original position by bioturbators, predators, or scavengers, but have not been transported out of their original community, and foreign remains that have been derived from other communities.

5. Bioturbation and physical reworking can also cause fossil assemblages to become time averaged (temporally mixed) and this *may* lead to increased diversity and morphological variation within and assemblage.

Of course, each of the points listed above represent types of bias in the fossil record, and they can greatly affect how data from a fossiliferous deposit are interpreted. As the science of taphonomy has matured, and the body of theory behind these principles has grown, it has become possible to begin predicting the utility of the fossil record for various types of evolutionary or paleoecological questions (Martin 1999). For example, it is now generally appreciated that studies of the ecological aspects of a fossil assemblage, such as population dynamics, should only be done on assemblages that were rapidly buried thereby minimizing the temporal and spatial mixing that could lead to incorrect interpretations. In this way, and many others, paleontologists have begun using their knowledge of the biases imposed on the fossil record by taphonomic processes to interpret the history of the formation of fossil assemblages.

In addition to the biases that can be grouped under the heading of taphonomy, there is another set of biases that can greatly affect the quality of the information that can be obtained from the fossil record. This second group of biases can be broadly grouped under the heading of worker biases, or biases due to sampling, processing, or analysis of data from the fossil record. While this type of bias is certainly not unique to paleontology, it has, nevertheless, become an active area of paleontological research in the last several decades. Through research on worker bias, it has been appreciated that the apparent patterns in the fossil record may be reflective of nothing more than where paleontologists choose to look (Sheehan 1977), or where and from what time periods rocks are preserved (Raup 1976; Peters and Foote 2001). Developing a better understanding of these types of biases can give paleontologists insight into the veracity of the patterns that are seen in the fossil record.

This dissertation focuses on both of types of bias listed above. Specifically, in the chapters that follow, several specific biases and their implications for the fossil record will be discussed. Each of the three chapters focus on the fossil records of bivalves and brachiopods and in two of three chapters, the fossil records of these two common marine organisms will be compared to gain additional insight into the quality of the record.

In chapter one, the deleterious effects of time averaging are explored in the sub-fossil record of an extant brachiopod species. Specifically, this chapter focuses on the recognition of morphological variability in the fossil record, and the fidelity between the life and death

assemblage with respect to this parameter. To explore this issue, several geometric morphometric techniques are employed that enable quantification and direct comparison of morphology between different populations. The fidelity of the fossil record, used here to refer to how closely, or accurately, the fossil record captures original biological information (Behrensmeyer et al., 2000), is a branch of research on time-averaging that has been particularly successful, but has been under-investigated. The brachiopod that is the focal point of chapter one, *Terebratalia transversa* is extremely morphologically variable in all known living populations and this research was undertaken to determine if this high degree of variability could be recognized in the fossil record of this species.

The results from several geometric morphometric techniques (including procrustes analysis and thin-plate spline) confirm a high degree of morphological variability with little change in mean shape between the living and sub-fossil assemblage. Additionally, there is no evidence of distinct morphogroups in either assemblage, as postulated for the species in previous studies (Schuman 1990). These trends persist at all depths and size classes. The similar range of morphological variability at each site suggests a common causal factor such as a similar array of micro-environments available at all depths. Another implication of this consistency between the living and the dead assemblage is that the variability of a fossil assemblage of this species could be used to estimate single-generation variability during the time averaged interval. Finally, it is encouraging to note that, given the full range of morphological variability in the fossil record of this brachiopod, this species could be recognized as a single, rather than multiple, species if only fossil data were available.

The second chapter involves the recognition and quantification of an underappreciated worker bias in the published literature on brachiopods and bivalves. This bias involves the images of specimens that are published in descriptions of species or faunas. Such images are an important and relatively untapped resource for paleontologists. Among other things they can provide a vast amount of data on body size evolution to the researcher that takes simple measurements of the images. However, before images in the published literature can be used in this manner, any difference in the average size between photographed specimens and the populations from which these specimens were drawn must be evaluated and quantified. This is the focal point of chapter two. Specifically, the quality of data from published images is assessed therein with respect to three parameters: (1) bias direction – the presence of non-random departures from the actual mean size of a species; (2) bias magnitude – the absolute value of the

mean departure, that is, the imprecision of the data; and (3) bias consistency – the variation in the direction and magnitude of bias within and across monographs, higher taxa, or time intervals. With a clear understanding of these bias parameters it is possible to assess the utility of monograph-derived size data.

Finally, chapter three is a comparative study of assemblages of sympatric Holocene bivalves and brachiopods from a modern tropical shelf (Southeast Brazilian Bight, South Atlantic). This study is one of the first to quantify the magnitude of time averaging (the amount of temporal mixing) for two different organisms collected from the same sites. Quantification of time averaging is accomplished by dating a suite of shells from each site using amino acid racemization calibrated with several AMS radiocarbon dates. By studying the age distributions for each species at each site it is determined that, despite some site to site differences, both bivalve and brachiopod species exhibit a very similar time averaging magnitude when collected from the same region and/or depositional system. Furthermore, by comparing the data described in chapter three with other previously published data of the same type, but from different depths and depositional systems, a significant correlation between depth and duration of time averaging is noted. This finding provides a basis for the third general principle of taphonomy (mentioned above) that shallow water skeletal assemblages are more susceptible to the processes of taphonomic destruction than are deeper water assemblages. This translates into a greater time averaging magnitude for deeper water assemblages because skeletal elements can survive longer in these environments. The most striking thing about this pattern is that it is very similar for vastly different depositional environments and latitudes, indicating that a wide array of skeletal assemblages may follow this pattern of increasing time averaging magnitude with increasing depth.

ATTRIBUTION

Each of the following chapters has been prepared with the goal of eventual publication in peer-reviewed journals. Chapter one has already been published (Krause 2004), chapter two was submitted in November of 2005, and chapter three will be submitted in May of 2006.

Chapter one is published as a single-authored work. As such, 100% of the work behind chapter one was done by R. A. Krause. Chapters two and three, when published, will be published as multiple authored papers because these studies represent portions of ongoing collaborative studies. However, the coauthors for these papers (listed on the title page for each chapter) contributed less than 20% to the data collection, analysis, and writing for these papers. As a result, these chapters can be considered to be mostly the work of R. A. Krause, which justifies their inclusion in this dissertation.

ACKNOWLEDGEMENTS

Field work for chapter one was conducted while participating in a course in Invertebrate Taphonomy during summer, 2002 at Friday Harbor Laboratories of the University of Washington. The organizers of the course, M. Kowalewski and M. LaBarbera, and the T.A., T. Rothfus, offered countless hours of help and support, without which this project could not have been completed. The faculty and staff of Friday Harbor Laboratories also provided invaluable financial and technical support, especially C. Staude, captain of the R/V *Nugget* during sampling voyages. The detailed peer reviews of M. Sandy and two anonymous reviewers greatly improved the structure and methodology of the study.

For assistance with the second chapter, I would like to thank John Alroy, Colin Sumrall, and Steve Wang for helpful discussions. John Pojeta and Lauck Ward provided hospitality and logistical support during research visits to the National Museum of Natural History and the Virginia Museum of Natural History, respectively. Susan Barbour-Wood helped with some of the data collection. Generous financial support was provided by the Paleobiology Database and the Department of Geosciences at Virginia Tech.

The third chapter benefited from discussions with M. Carroll and D. Rodland. I also thank M. Carroll for allowing access to her data. This project was funded by National Science Foundation grants, EAR0125149 (Kowalewski) and EAR124767 (Goodfriend [then Wehmiller]), and by a Research Grant from the Petroleum Research Fund of the American Chemical Society (AC-PRF#40735-AC2) to Kowalewski.

CHAPTER ONE¹: An Assessment of Morphological Fidelity in the Sub-fossil Record of a Terebratulide Brachiopod

¹ This chapter has been published in a peer reviewed journal:
Krause, R.A., Jr. 2004. An assessment of morphological fidelity in the sub-fossil record of a terebratulide brachiopod. *Palaios* 19: 460-476.

ABSTRACT

The process of time-averaging can have deleterious effects on the recognition of morphological variability in the fossil record. To explore this issue, a geometric morphometric study was conducted on a life and death assemblage of the terebratulide brachiopod *Terebratalia transversa* (Sowerby, 1846).

The results from several geometric morphometric techniques (including procrustes analysis and thin-plate spline) confirm a high degree of morphological variability with little change in mean shape between the living and sub-fossil assemblage. Additionally, there is no evidence of distinct morphogroups in either assemblage, as postulated for the species in previous studies. These trends persist at all depths and size classes. The similar range of morphological variability at each site suggests a common causal factor such as a similar array of micro-environments available at all depths.

One implication of this consistency in morphological variability between the living and sub-fossil assemblage is that the variability of a fossil assemblage of this species could be used to estimate single-generation variability during the time averaged interval. Furthermore, the potential for recognizing the full range of shape variability in the sub-fossil record of a highly variable species is encouraging for the pursuit of species recognition in the fossil record. The very good fidelity of the sub-fossil assemblage with respect to morphological variability is documented here for the first time in brachiopods, and agrees well with the findings of similar studies of other taxa.

INTRODUCTION

Time-averaging of skeletal accumulations - an important process that affects many of the parameters that paleontologists estimate from the fossil record, including diversity, paleoecology, evolutionary rates, and morphospace occupation - has received much attention in recent years (Kidwell, 1986; Kidwell and Bosence, 1991; Kidwell and Brenchley, 1994; Kowalewski, 1996; Olszewski, 1999; Behrensmeyer et al., 2000; Bush et al., 2002). Quantitative estimates of time-averaging durations are now available for some organisms, primarily mollusks, in some environments (Flessa et al., 1993; Flessa and Kowalewski, 1994; Meldahl et al., 1997; Kowalewski et al., 1998). One branch of research on time-averaging that has been particularly successful, but is in some ways under-investigated, is the evaluation of the fidelity of the fossil record with respect to certain parameters. Fidelity is used here to refer to how closely, or accurately, the fossil record captures original biological information (Behrensmeyer et al., 2000). With respect to a given fossil assemblage, the fidelity of a number of different parameters can be evaluated. For example, depending on the research question, one could conceivably investigate biochemical, anatomical, spatial, and/or compositional fidelity (Kidwell and Bosence, 1991; Behrensmeyer et al., 2000).

This study focuses on the morphological fidelity of a sub-fossil assemblage of the terebratulide brachiopod *Terebratalia transversa* (Sowerby, 1846). Theoretical models of the effects of time-averaging on morphology indicate that under certain taphonomic conditions, variance can be either overestimated or falsely partitioned into discrete groups (by removing certain morphs), potentially resulting in the designation of several species from one, if only fossil data are available (Kidwell, 1986; Bush et al., 2002). A recent morphometric study of the bivalve genus *Mercenaria* (Bush et al., 2002) showed that morphological variance is consistent from extant populations to their sub-fossil record. However, *Mercenaria* is durable and exhibits a rather low degree of morphological variability. To fully understand the effects of time-averaging on morphology, and to evaluate the morphological fidelity of assemblages with multiple taxa, it is necessary to study species that exhibit a high degree of morphological variability and vary in fossilization potential. It is also imperative that studies of organisms from other phyla be conducted, as much of the time-averaging literature on shelly benthic invertebrates only considers mollusks.

Herein, geometric morphometric techniques are applied to an extant terebratulide brachiopod in order to assess the morphological fidelity of its sub-fossil assemblage. The goals of this study are two-fold. The first part of this paper will focus on the description and quantification of morphological variation in the extant brachiopod *Terebratalia transversa*, specifically focusing on differences that may be present between the living population and the sub-fossil assemblage. The validity of previously defined morpho-groups will also be evaluated. The second part of the paper will explore patterns found in the context of an intrinsic factor (size) and an extrinsic factor (depth). Both of these goals have direct implications for the development of models that assess the ‘filtration’ of morphology from living populations to sub-fossil to fossil record.

Previous Work

The terebratulide brachiopod *Terebratalia transversa* is very abundant in the deep, narrow, glacially-scoured channels around the San Juan Islands of northwestern Washington State, USA. Because it is such a common element of the local fauna, and because of the close proximity of a major marine biological research station (Friday Harbor Laboratories of The University of Washington), this brachiopod has been relatively well studied by workers of diverse interest and background (Shimer, 1905; Du Bois, 1916; Paine, 1969; Thayer, 1975, 1977; LaBarbera, 1977; Stricker and Reed, 1985a, b; Rosenberg et al., 1988; Alexander, 1990; Schumann, 1990; Daley, 1993)

The large degree of morphological variation exhibited by this species has been noted by several workers (Du Bois, 1916; Paine, 1969; Schumann, 1990), and is best described by Paine (1969) who noted that variants ranged “...from prolate to oblate spheroids, with well defined to poorly defined sulci, with smooth or ribbed shells, and with other variable characters.” Such variation would seem to go beyond the bounds of typical intraspecific variation. Indeed, a more recent study by Schumann, (1990) indicated the presence of morpho-groups, which he defined by noting the order of brachiopod to which certain shells bore a close resemblance. For example, the ‘Spirifer’-type is alate with a wide hinge line and distinct radial ribs (Schumann, 1990). The ‘Atrypa’ and ‘Terebratula’ types represent more globose forms with variable degrees of ribbing. These forms often exhibit a high degree of asymmetry, especially in environments with high velocity currents (Schumann, 1990). It has been postulated (Du Bois, 1916; Schumann, 1990) that these distinct morpho-groups resulted from exposure to different environmental conditions,

mainly current velocity. Following this model, larval *Terebratalia transversa* would only settle in low current regimes, and individuals would not encounter higher currents until later in development when they grow large enough to be above the boundary layer. This has in fact been demonstrated experimentally by LaBarbera (1977) who noted that larval *T. transversa* will not metamorphose in currents higher than 0.25 cm/s. Considering that currents in the San Juan Channel can be as high as 2m/s (Thayer, 1975), it would seem that larvae would have to settle in protected areas, perhaps on the lee side of large pebbles or large colonies of balanid barnacles which are abundant in some places. Once settled these individuals do not reorient themselves in response to changing current direction or velocity (Thayer, 1975, 1977; LaBarbera, 1977), and therefore must cope with the currents that are presented to them. Schumann (1990) postulated that morphological variants result from these differences in orientation to current.

The drawback of Schumann's and other studies describing morphology of *Terebratalia transversa* is the reliance on completely qualitative data. People have an innate sense of pattern recognition, even when there is no pattern. Because of this, other techniques are needed to back up what one thinks one sees.

Geometric morphometric methods have, during the last decade, been increasingly applied to various problems involving shape and shape change in organisms (Bookstein, 1990, 1991, 1996; Chapman, 1990; Marcus et al., 1996; Rohlf, 1990a, b, 1996, 1999; Rohlf and Slice, 1990; Dryden and Mardia, 1998). When applied correctly they can be a very powerful tool for the study of evolution in many different contexts. This study represents a first attempt to quantitatively define shape variability of *Terebratalia transversa* using geometric morphometric methods and to track them from the life to the death assemblage at several sites along a bathymetric gradient.

MATERIAL AND METHODS

Sample Collection

Samples were collected along a steep bathymetric gradient on a transect across the San Juan Channel between Rock Point and Griffin Bay in the vicinity of San Juan and Lopez Islands (Fig. 1.1). Each sample was taken using a mud dredge, which sampled the benthic assemblage continuously through an area of roughly 45 m². All dredging was done parallel to depth contours so as not to mix assemblages from different depths. Nine dredge samples were taken in total,

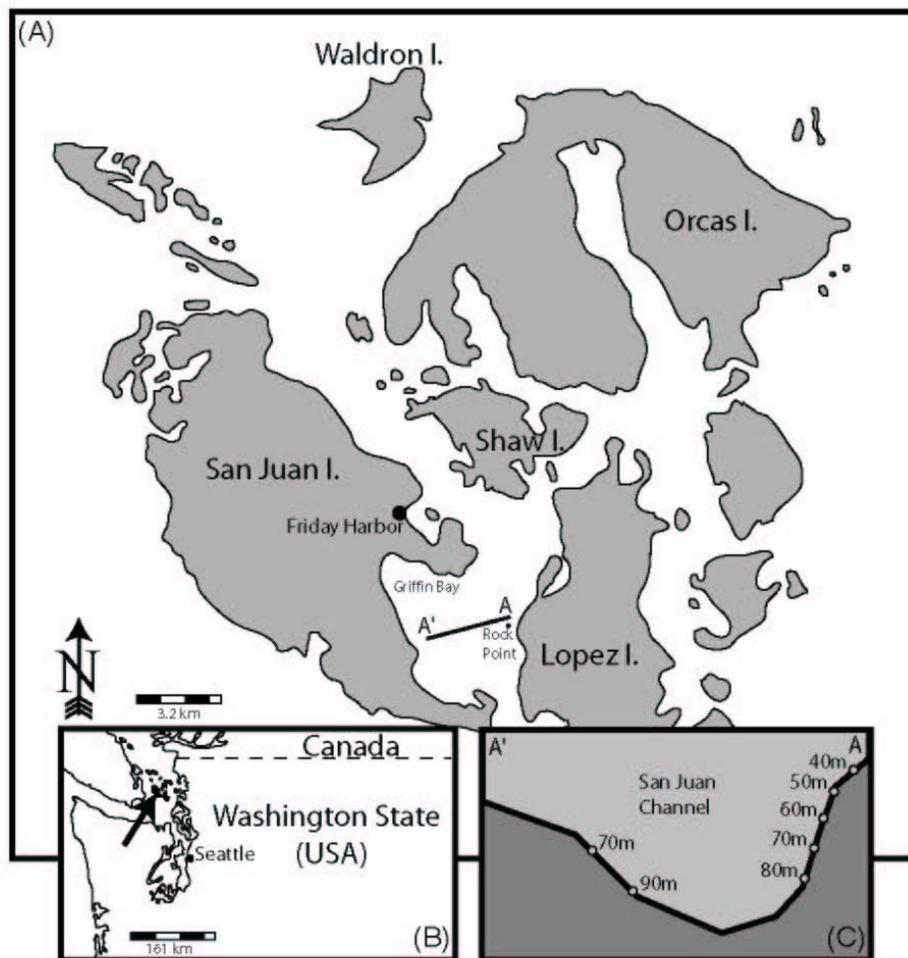


Figure 1.1 – Location map. (A) San Juan Islands showing location of Friday Harbor Research Station and sampling transect A-A'. (B) Regional setting of San Juan Islands in Puget Sound roughly 160 km NW of Seattle. (C) Simplified cross section of San Juan Channel showing sampling transect A-A'.

Table 1.1 - Depth distribution of samples.

Depth	Live	Dead	Total
40m	10	11	21
50m	6	10	16
60m	1	6	7
Shallow (40-60m)	17	27	44
70m	28	40	68
80m	41	19	60
Deep (70-80m)	69	59	128
Total	86	86	172

ranging from 20-120 m. From these samples, a total of five depth groups (40m, 50m, 60m, 70m, and 80m) yielded abundant specimens of *Terebratalia transversa*. The majority of the specimens were from the east side of the San Juan Channel (Fig. 1.1C), but some came from the shallower sloped western side of the channel. However, sample sizes were not sufficient on the western side to create ‘stand alone’ samples, so samples from 70m on the western side were grouped with 70m samples from the eastern side and samples from 90m on the western side were grouped with samples from 80m on the eastern side. This procedure is justified by the similarity of sediment size fractions (mostly cobbles and boulders) in the dredge samples from which material for this study was obtained. For further discussion of environments along the transect see Kowalewski et al. (2003) and Rothfus et al. (in prep.).

Both live and dead specimens were collected from each dredge that yielded brachiopods. For consistency, only whole, articulated shells of *Terebratalia transversa* were chosen for morphometric analysis. For the purpose of simplifying analyses, an equal number of live and dead shells were chosen. In all samples there were fewer dead, articulated shells than live shells. Thus, the number of useable dead shells was the limiting factor when assembling specimens for analysis. A total of 172 shells were analyzed ($n_{\text{Live}}=86$; $n_{\text{Dead}}=86$). The distribution of the shells by depth is given in Table 1.1.

Data Collection

Specimens were imaged in two orientations using a Polaroid DMC 1 digital camera. For the anterior view, each specimen was placed with the anterior up and the camera was oriented parallel to the commissural plane (Fig. 1.2A). For the dorsal view, each specimen was placed with the dorsal (brachial) valve up and the camera was oriented perpendicular to the commissural plane (Fig. 1.2B).

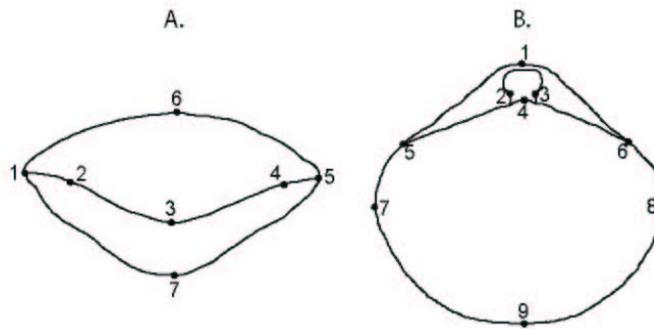


Figure 1.2 - Two views of *Terebratalia transversa*, showing landmark locations. (A) Anterior view. (B) Dorsal view. For landmark descriptions see Table 1.2.

Morphometric analyses presented here are based on two sets (one for each view) of landmarks and pseudolandmarks that were taken on each shell. Seven landmarks were used for the anterior view and nine were used for the dorsal view (Fig. 1.2, Table 1.2). Both true landmarks and pseudo-landmarks (Type I and II respectively) were used together in both views to maximize the ability to quantify shape differences between individuals. The usefulness of combining different types of landmarks in the same analysis varies with the question being asked (Bookstein, 1990, 1991). In this study, a mix of homologous points and geometric points were considered necessary to fully capture the morphological variation of the organism. This methodology is justified by the operator error study (discussed below) which shows equal scatter of replicates around Type I and Type II landmarks. Landmarks were taken using the image analysis program SCION Image for Windows beta 4.0.2, developed by the U.S. National Institutes of Health and Scion Corporation and available as freeware from <http://www.scioncorp.com>.

External views were used exclusively because morphological differences among individuals of *Terebratalia transversa* are most easily recognized in external properties of the shell. Also, previous analyses of the morphology of *T. transversa* all used external features exclusively, to define morpho-groups.

Table 1.2 - Landmark descriptions.

Landmark	Type	Location
Anterior view		
1	II	Leftmost adjoining point between dorsal and ventral valve
2	II	Point of maximum curvature of the commissure between landmarks 1 and 3
3	II	Ventralsmost point of maximum curvature of sulcus
4	II	Point of maximum curvature of the commissure between landmarks 3 and 5
5	II	Rightmost adjoining point between dorsal and ventral valve
6	II	Point of maximum curvature of dorsal valve near the plane of symmetry
7	II	Point of maximum curvature of ventral valve near the plane of symmetry
Dorsal view		
1	II	Posteriormost point of ventral umbo
2	I	Left-lower margin of pedicle foramen
3	I	Right-lower margin of pedicle foramen
4	II	Posteriormost point of dorsal umbo
5	I	Left-lateral adjoining point of interarea and dorsal valve
6	I	Right-lateral adjoining point of interarea and dorsal valve
7	II	Leftmost point of maximum curvature
8	II	Rightmost point of maximum curvature
9	II	Anteriormost point of maximum curvature of dorsal valve

Analytical Methods

Procrustes Analysis: Shape was analyzed for both views using Procrustes analysis, a superimposition technique that allows the comparison of landmark configurations by overlaying one on top of the other. There are several different variants of Procrustes analysis, each useful for a specific set of circumstances (Bookstein, 1990, 1991, 1996; Chapman, 1990; Rohlf, 1990b, 1996, 1999; Rohlf and Slice, 1990). For this study, a Generalized Least Squares Full Procrustes Analysis (GLS-FPA) was utilized. This procedure calculates a reference (mean) configuration from all of the samples. Each configuration of landmarks, corresponding to each sample, is then rotated, translated and rescaled such that the distance from each sample to the reference configuration is minimized using a least squares algorithm. In full Procrustes analysis, centroid size is used to rescale each configuration to control for differences in size. Centroid size is defined as the square root of the summed squared distances from each landmark to their common

centroid (Dryden and Mardia, 1998). It is a very convenient measure of overall size of an organism because it is uncorrelated with shape variables and thus cannot indicate allometry when none is present. Because of this, centroid size was also used later in the analysis to correct for allometry in variability estimates. The SAS/IML code used for least squares Procrustes analysis was modified from a code written by M. Kowalewski and A. Bush (Bush et al., 2002).

To graphically display the results from the Procrustes analysis, the partial tangent coordinates were plotted on an x-y scatterplot. In most cases, especially where it was desirable to show the relationship of several groups on one superimposition plot, the data points themselves were omitted and replaced with polygons encircling their distribution. This was done to improve the clarity and readability of these plots.

Comparison of fitting techniques: Least squares Procrustes analysis (GLS-FPA) is regarded as the approach of choice when variance in shape is spread more or less equally among landmarks (Chapman, 1990), that is, no particular landmark has more variance than the others. In situations where change in shape is localized to one or a few landmarks, a different Procrustean method must be used. In order to evaluate the appropriateness of two different fitting techniques for the data presented here, a Resistant Fit-Full Procrustes Analysis (RF-FPA) was also run on the landmark data for both shell views using Resistant-Fit Theta-Rho-Analysis, available with the program CoordGen6, which is part of the Integrated Morphometrics Package (IMP) developed by D. Sheets and available as freeware at <http://www.canisius.edu/~sheets/morphsoft.html>.

The results of both analyses are very similar (Fig. 1.3) indicating a roughly equal spread of variance across all landmarks in both shell views. Therefore, the Least Squares method was used exclusively for the remainder of the study because outputs from GLS-FPA can be easier to deal with in multivariate analysis than those from RF-FPA.

Operator Error Estimation: Repeatability is a potential problem in most morphometric studies. Whether one's primary unit of investigation is a specimen or a photograph, substantial error can be introduced to the experiment if a standardized procedure is not used consistently.

To assess the amount of operator error involved with all of the stages of this analysis, one shell from each of four randomly chosen sites was selected, re-imaged and re-measured ten times. Each replication for each shell was done on different, non-consecutive days. Shells were chosen so that two live and two dead samples would be replicated, and both views were replicated for all four samples. The ten replicates for each shell view were pooled with the full

dataset and subjected to Procrustes analysis. The results from two of the replications are shown in Figure 1.4. The tight grouping of replicate landmarks in each case indicates that measurement error is slight in comparison to total morphological variability (for the variability values of the replicates, see Table 1.3). Additionally, the equal scatter around Type I and Type II landmarks provides justification for using both types together in this study.

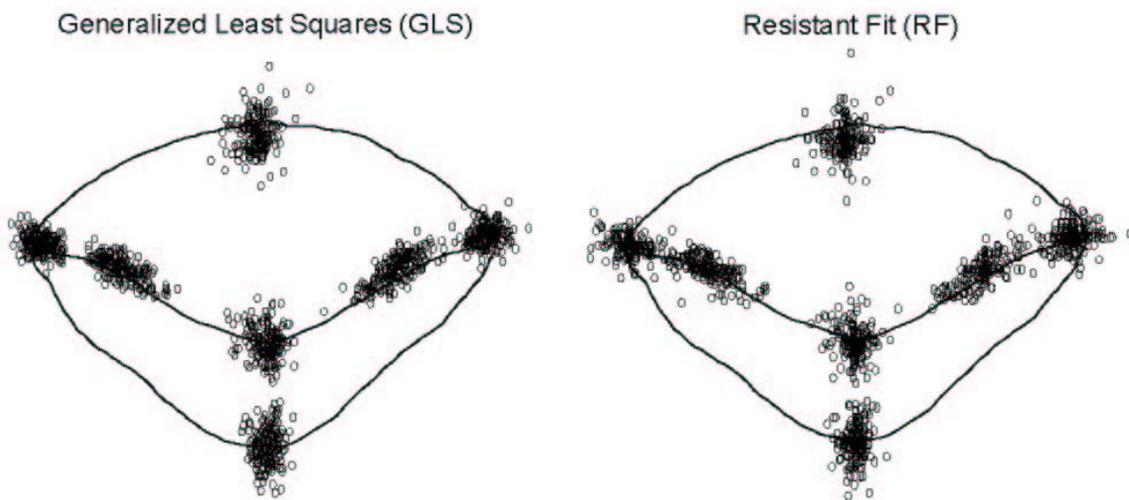


Figure 1.3 - Procrustes superimposition of anterior landmark configurations. Two different fitting techniques are shown here. (A) GLS=Generalized Least-Squares; (B) RF=Resistant Fit Theta Rho Analysis

Principal Components Analysis: Another way to examine the variability of landmark points in tangent space is to run a principal components analysis (PCA) on the tangent coordinates derived from Procrustes analysis. In fact, this method may be more reliable for visualizing variation in landmarks than superimposition methods even though it does not allow examination of variation at single landmark positions.

Tangent coordinates for each shell view (anterior and dorsal) were analyzed in the PROC PRINCOMP procedure available in SAS 8.02 using the covariance matrix option. Scores for the first three principle components were then plotted on bivariate scatterplots (Figs. 1.5-1.6).

Canonical Variates Analysis: For the purpose of comparing mean shapes, Canonical Variates Analysis (CVA) was used. Again, the tangent coordinates for both views were the two datasets used for this analysis. Prior to running CVA, the tangent coordinate matrix for each

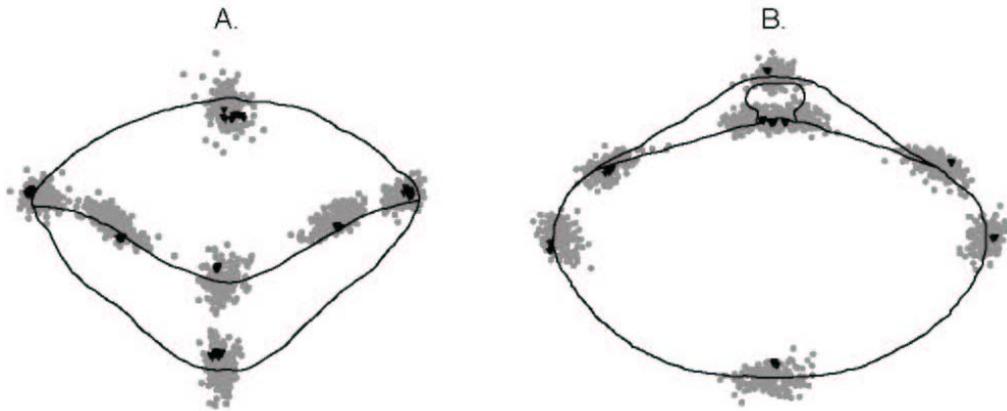


Figure 1.4 - Two of the replications done for operator error estimation. (A) Anterior view replicates; sample D107L. (B) Dorsal view replicates; sample B102D. Black points show ten replications of each configuration. Grey points represent the entire dataset for each view.

view had to be pared down because the tangent coordinates (as well as the full Procrustes residuals) are subject to four almost-linear constraints (Bookstein, 1996). Because of these constraints, inversion of the covariance matrix yields meaningless coefficients (Bookstein, 1996; Rohlf, 1999). One of the ways to avoid this pitfall, which is used here, was outlined by Bookstein (1996) and by Rohlf (1999). Two vectors (four eigenvalues) from the tangent coordinates must be removed. In principle, any four eigenvalues can be removed, however, Rohlf (1999) recommended removal of the four smallest values as they account for very little of the variation in the dataset. This recommendation was followed here. PCA was run on each of the tangent coordinate datasets and the four smallest eigenvalues were removed in each case. CVA was then run on the pared-down datasets.

Table 1.3 - Variability values for the replicate samples.

	N	Total Variability	Allometry Free Variability
Dorsal View			
B102D	10	0.0127	0.0117
C106D	10	0.0174	0.0141
D107L	10	0.0212	0.0189
E117L	10	0.0262	0.0253
Anterior View			
B102D	10	0.0304	0.0253
C106D	10	0.0278	0.0277
D107L	10	0.0291	0.0266
E117L	10	0.0312	0.0265

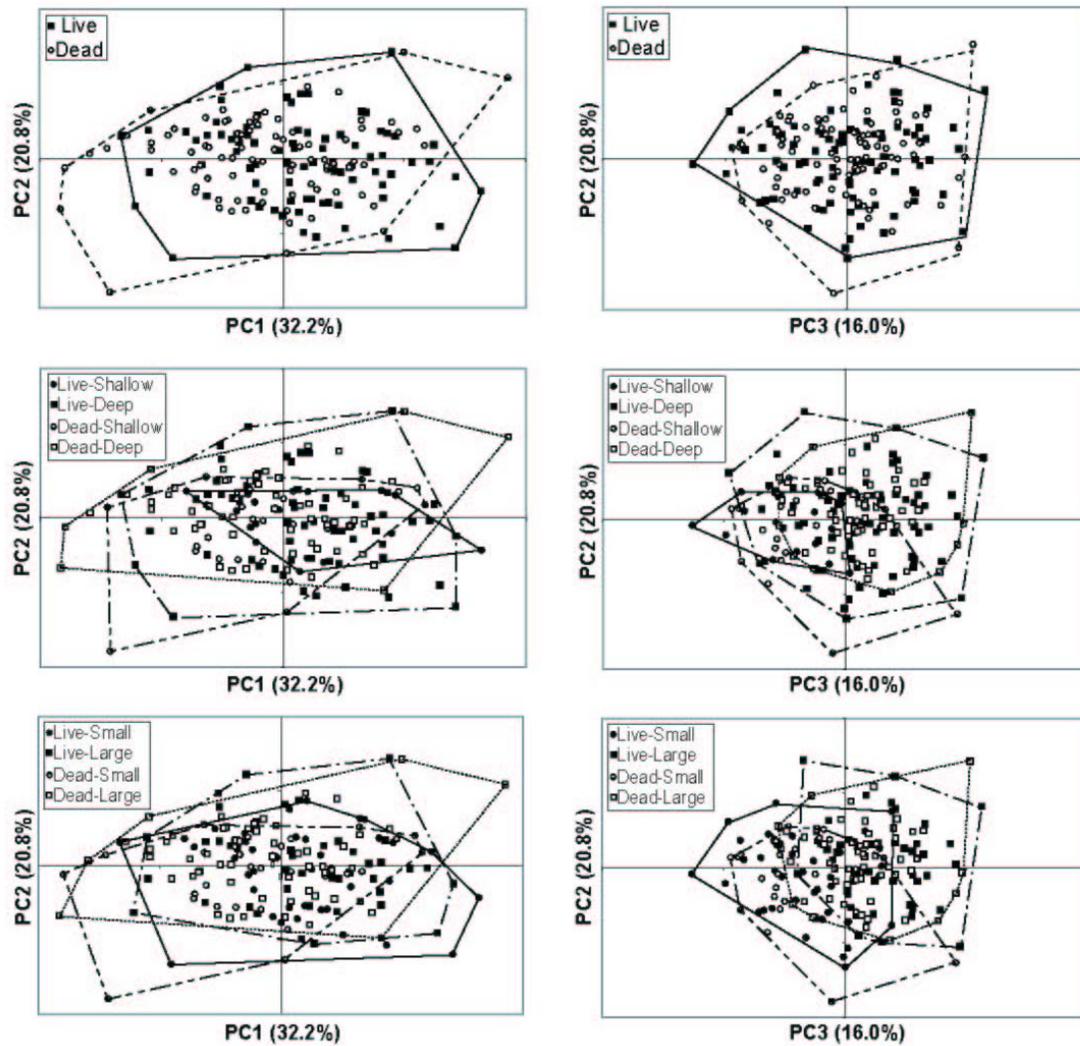


Figure 1.5 – Bivariate scatterplots of scores from the first three axes of principle components analysis for the anterior shell view. Data are grouped by live-dead, depth groups, and size groups (from top to bottom).

Canonical Variates Analysis requires that *a priori* groups be designated in a dataset. The CVA then attempts to maximize the difference between these groups in ordination space. Importantly, axes derived from a CVA are not orthogonal to each other as they are in PCA, and thus the distance between any two points is distorted (Marcus, 1990). Distinctness of groups is then evaluated with a MANOVA on Mahalanobis Distances (D^2) between the centroids of the *a priori* designated groups (Table 1.5). However, it is also important to note the variability of each group in the ordination space. The Mahalanobis distance between two groups may be significant, but if the variability of the groups is such that they substantially overlap then it may be difficult to argue for distinctness of the groups.

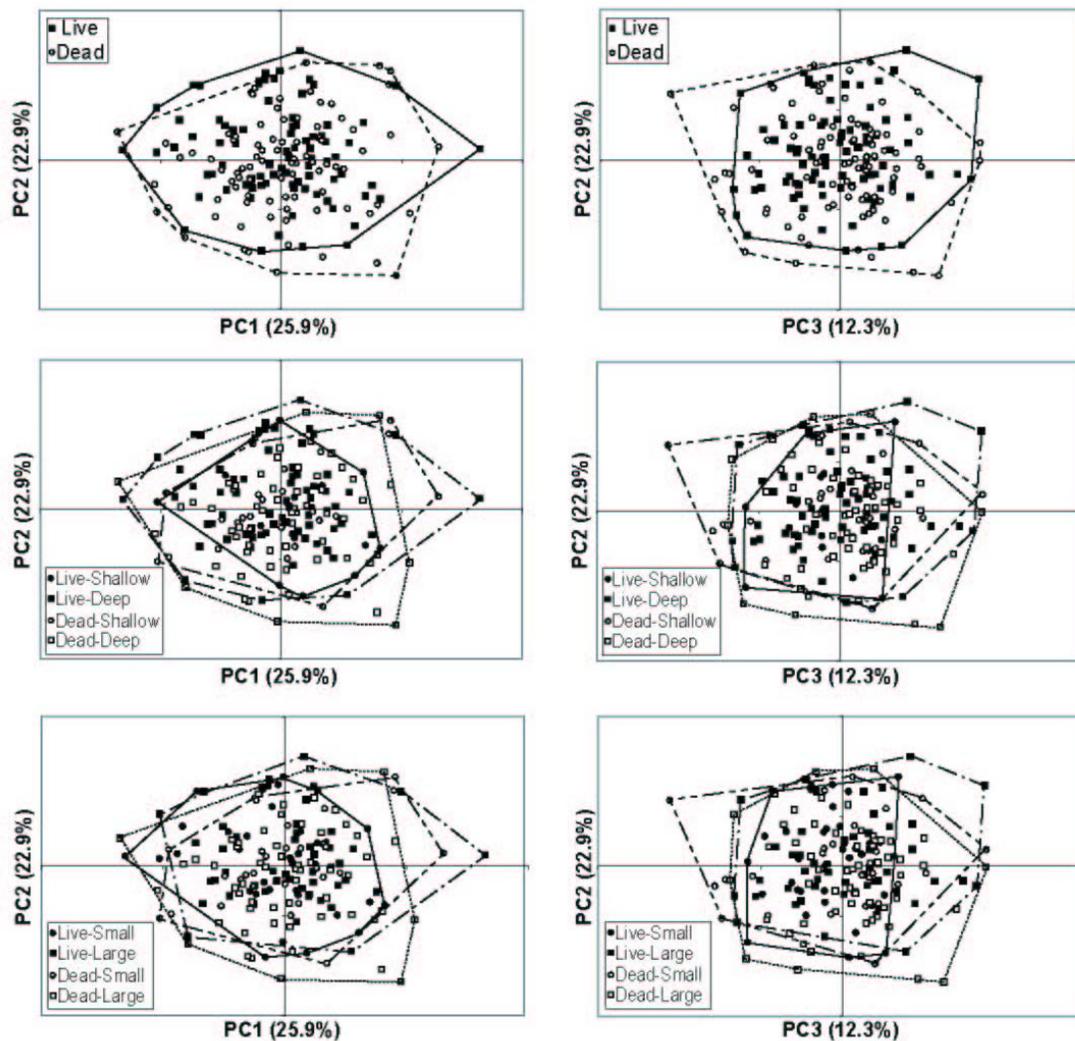


Figure 1.6 - Bivariate scatterplots of scores from the first three axes of principle components analysis for the dorsal shell view. Data are grouped by live-dead, depth groups, and size groups (from top to bottom).

A total of four canonical variates analyses were run for this study. Each dataset (anterior and dorsal) was run twice, first with depth groups designated and then with size groups designated. These groupings will be explained later in the text. Scores for the first two canonical axes (CV1 & CV2) were then plotted on bivariate scatterplots and groups were indicated with polygons encircling the data points (Fig. 1.7).

Thin-Plate Spline Analysis: Another method of comparing mean shapes is the geometric morphometric method of thin-plate spline analysis (TPS)(Bookstein 1990; 1991; 1996). TPS can be very useful for visualizing the magnitude and direction of change between two shapes.

The two shapes used for this analysis were the mean landmark configurations from the Live and Dead groups. The analysis was run using the program tpsSpln version 1.18 developed by F.J.

Rohlf, and available as freeware at <http://life.bio.sunysb.edu/morph>. The results from the TPS are shown in Figure 1.8B, and will be discussed below.

Variability Metrics: To examine the variability of the landmarks fitted using least squares Procrustes, there are numerous procedures one can use (Dryden and Mardia, 1998). The measure of variability employed herein uses the partial Procrustes tangent coordinates and the mean (consensus) configuration of landmarks, each derived from the Procrustes analysis. The tangent coordinates are obtained by projecting points in a non-Euclidean shape space, which is utilized by landmark morphometrics, often referred to as Kendall's Shape Space (but see Slice, 2001) into a Euclidean space that is tangent to it. The mean configuration is then simply the mean point at each landmark position. The variability measure is calculated as the square root of the mean squared distances of the partial tangent coordinates for each landmark on each specimen to the mean shape. Thus, each specimen is assigned a unique variability value, but in order to be meaningful, the discussion in this paper will be limited to groups of shells and their mean variability values.

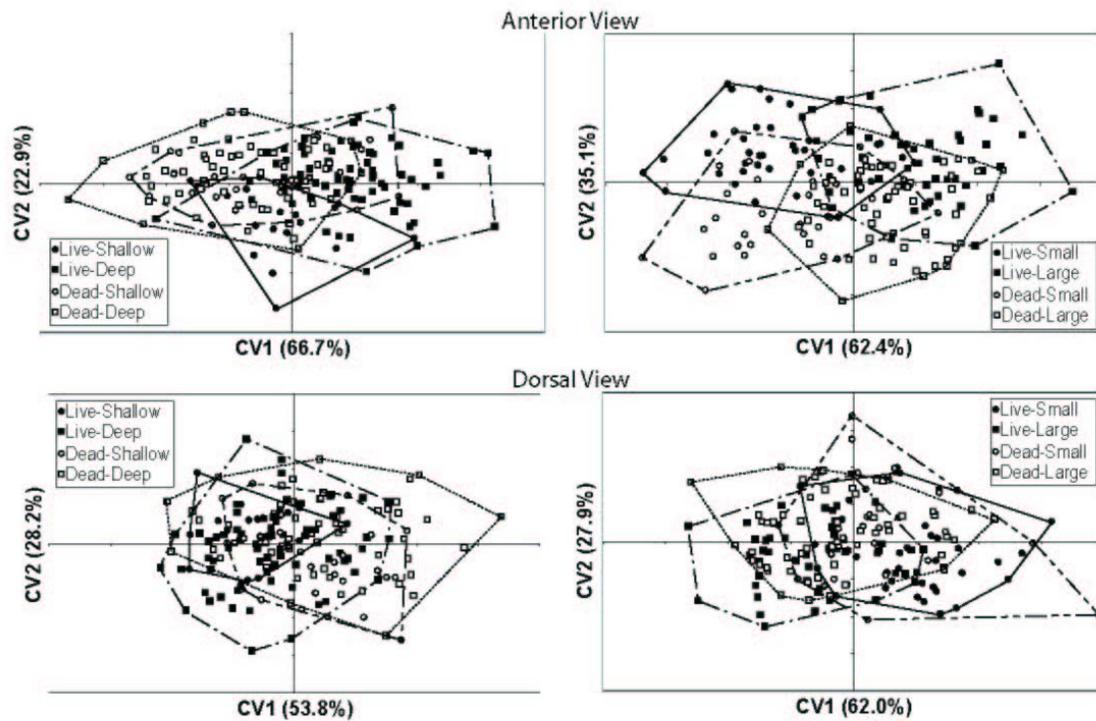


Figure 1.7 – Bivariate scatterplots of scores from the first two axes of a canonical variates analysis. Data for both shell views are shown, grouped by depth and by size.

Like many organisms, *Terebratalia transversa*, grows allometrically. The effects of this shape change with growth will be discussed in further detail below, although an exhaustive treatment is beyond the scope of this paper. Because of allometric growth, all of the size-related variability is not removed by the normal Procrustes operation of setting each configuration to unit centroid size. There is still some amount of shape variability due to size that is included in the partial tangent coordinates. One way to remove the allometric component, and thus obtain an allometry-free variability, is to regress the partial tangent coordinates on centroid size (Dryden and Mardia, 1998). After the correction for allometry, the square root of the mean squared distances was again calculated to yield allometry free variability (Table 1.3, 1.4).

Finally, all statistical analyses performed for this study utilize an arbitrarily selected significance level (α) of 0.05.

Table 1.4 - Total and Allometry-free variability values for samples grouped by live-dead, depth, and size.

	N	Total Variability	Allometry Free Variability
Dorsal View Variability			
Pooled	172	0.0979	0.0972
<i>Live</i>	86	0.0939	0.0928
<i>Dead</i>	86	0.1011	0.1004
40m	21	0.0867	0.0818
<i>Dead</i>	11	0.0848	0.077
<i>Live</i>	10	0.0862	0.0798
50m	16	0.1006	0.0946
<i>Dead</i>	10	0.1053	0.0991
<i>Live</i>	6	0.0869	0.0757
60m	7	0.0954	0.0814
<i>Dead</i>	6	0.0869	0.0757
<i>Live</i>	1	.	.
70m	68	0.0993	0.0983
<i>Dead</i>	40	0.1022	0.1012
<i>Live</i>	28	0.0936	0.0916
80m	60	0.0966	0.0952
<i>Dead</i>	19	0.1006	0.0956
<i>Live</i>	41	0.0939	0.0917
Large Centroid	108	0.0971	0.0968
<i>Dead</i>	58	0.0994	0.0985
<i>Live</i>	50	0.0933	0.0925
Small Centroid	64	0.0979	0.0956
<i>Dead</i>	28	0.1032	0.1011
<i>Live</i>	36	0.0927	0.0891
Anterior View Variability			
Pooled	172	0.1169	0.1114
<i>Live</i>	86	0.1149	0.1067
<i>Dead</i>	86	0.1153	0.1112
40m	21	0.1042	0.0951
<i>Dead</i>	11	0.0876	0.0836
<i>Live</i>	10	0.115	0.0965
50m	16	0.1068	0.1012
<i>Dead</i>	10	0.1123	0.1012
<i>Live</i>	6	0.0863	0.0782
60m	7	0.1559	0.1432
<i>Dead</i>	6	0.1534	0.1186
<i>Live</i>	1	.	.
70m	68	0.1115	0.1071
<i>Dead</i>	40	0.1082	0.1048
<i>Live</i>	28	0.1082	0.1019
80m	60	0.1165	0.1077
<i>Dead</i>	19	0.1064	0.0993
<i>Live</i>	41	0.1158	0.1047
Large Centroid	103	0.1118	0.1109
<i>Dead</i>	57	0.111	0.1092
<i>Live</i>	46	0.1092	0.1074
Small Centroid	69	0.1142	0.1097
<i>Dead</i>	29	0.1153	0.1104
<i>Live</i>	40	0.1087	0.1022

Table 1.5 - Mahalanobis Distances (D^2) derived from canonical variates analysis, and associated p-values.

	Mahalanobis Distance (D^2)	F	P
ANTERIOR			
Live-shallow <> Live-deep	3.28	4.24	<0.001
Live-shallow <> Dead-shallow	2.77	2.74	0.004
Live-shallow <> Dead-deep	2.81	3.5	<0.001
Live-deep <> Dead-shallow	2.37	4.35	<0.001
Live-deep <> Dead-deep	2.94	8.85	<0.001
Dead-shallow <> Dead-deep	0.95	1.66	0.094
Live-small <> Live-large	4.71	9.55	<0.001
Live-small <> Dead-small	2.88	4.58	<0.001
Live-small <> Dead-large	4.92	10.94	<0.001
Live-large <> Dead-small	6.8	11.45	<0.001
Live-large <> Dead-large	1.88	4.54	<0.001
Dead-small <> Dead-large	3.16	5.75	<0.001
DORSAL			
Live-shallow <> Live-deep	0.81	0.72	0.749
Live-shallow <> Dead-shallow	1.73	1.19	0.29
Live-shallow <> Dead-deep	1.35	1.17	0.301
Live-deep <> Dead-shallow	0.77	0.99	0.468
Live-deep <> Dead-deep	0.66	1.38	0.168
Dead-shallow <> Dead-deep	0.65	0.79	0.678
Live-small <> Live-large	2.2	3.03	<0.001
Live-small <> Dead-small	1.2	1.25	0.246
Live-small <> Dead-large	1.87	2.73	0.001
Live-large <> Dead-small	1.94	2.3	0.007
Live-large <> Dead-large	0.71	1.26	0.24
Dead-small <> Dead-large	1.02	1.26	0.235

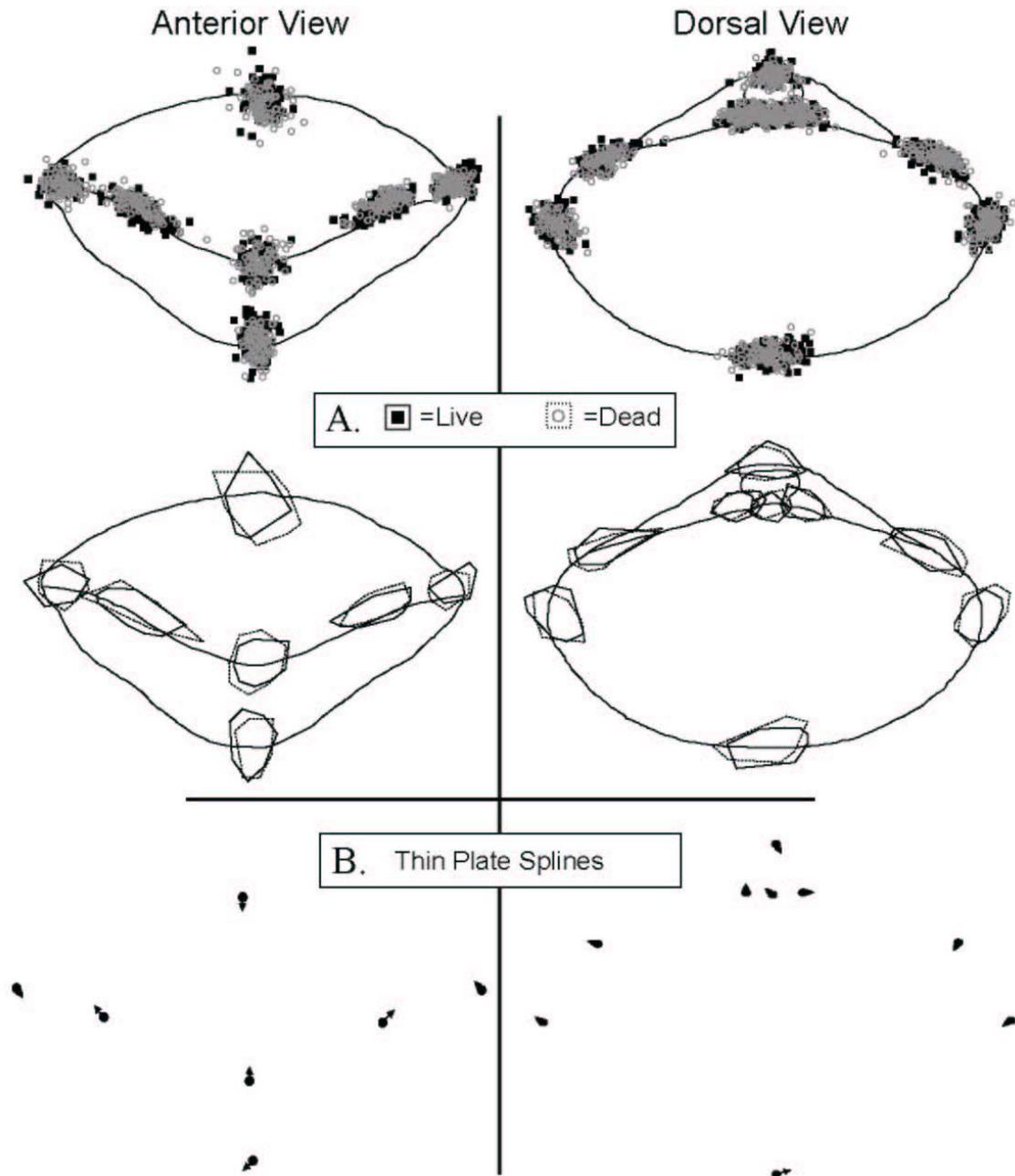


Figure 1.8 - Live-Dead comparisons of landmark configurations (n=172) fitted with Procrustes superimposition. (A) Superimposition plots of procrustes tangent coordinates for both shell views. Plots shown with all data points, and with encircling polygons showing their relative distributions. (B) Thin-plate spline vector plots. Arrows point from live mean configuration to dead mean configuration for each shell view.

RESULTS AND DISCUSSION

Mean Shape vs. Mean Variability

The results obtained for this study were arrived at through the use of a number of techniques each of which was designed either to compare mean shapes between groups (GLS-FPA, PCA, CVA, TPS) or to compare mean shape variability between groups (GLS-FPA, PCA, Allometry-free variability). Some of the techniques can accomplish both with varying degrees of success.

Through the course of this study it was determined that measures of morphological variability would be more informative than changes in mean shape for detecting differences between the time averaged assemblage and the standing crop population. Because the ‘dead’ or time averaged assemblage is a combined sample of many generations, it is the variability of that sample that must be examined to determine its degree of similarity, or fidelity, to the living population. Nevertheless, it is useful to examine mean shapes of different populations of *Terebratalia transversa* because much of the literature on this organism deals exclusively with this metric, although it is generally assessed qualitatively.

Live-Dead Comparisons

Results: The main focus of this study is the assessment of morphological fidelity of a sub-fossil assemblage of *Terebratalia transversa*. Consequently, those analyses that group the data into Live and Dead categories are potentially the most informative.

Scores from principal components analysis for each shell view, grouped by membership in Live and Dead categories, are shown in Figures 1.5 and 1.6. These plots show similar amounts of variance between the two categories, regardless of which view is examined. One possible exception is the plot of PC1 vs. PC2 for the anterior view (Fig. 1.5, top left panel). Dead shells may be more variable than Live shells based on the larger plot area encompassed by points of the Dead category. Additionally, the center of each cloud of points is in nearly the same position, demonstrating that mean shapes may not be different between live and dead shells. Furthermore, neither the live nor the dead groups have any discernible sub-groups present, suggesting a lack of distinct morphogroups in either of the assemblages. However, far reaching conclusions should not be drawn from such plots as PCA is not a confirmatory multivariate analysis.

Thin-plate spline analysis was also used to compare mean shapes between live and dead groups (Fig. 1.8B). In this analysis the mean configurations from Procrustes for each group was compared. The vectors shown in Figure 1.8B indicate the magnitude and direction of shape change at each landmark position from the live configuration to the dead configuration. As indicated by PCA, the amount of mean shape change between these groups (in both views) is minimal.

Potential shape variability changes between live and dead groups can be visualized by plotting the tangent coordinates of a full, generalized Procrustes analysis (Fig. 1.8A). The overlap between landmark configurations of both categories seems to be nearly complete, suggesting little difference in shape variability between live and dead specimen groups (allometry-free variability values are listed in Table 1.4). Additionally, the superimposition plots do not show distinct morphogroups for either shell view. To evaluate the statistical significance of the apparent similarity of variability for the two categories, 1000 mean allometry-free variability values and 95% and 99% confidence intervals around the actual means were calculated and compared for each group. This was accomplished with a 1000-iteration bootstrapping simulation written in SAS/IML by M. Kowalewski and modified by the author. The simulation was designed to randomly draw samples with replacement from a particular group in the dataset until the actual number of samples for that group was reached (e.g. n=86 for live and dead groups). The simulation then runs a GLS Procrustes analysis to compute a total allometry-free variability value for each iteration. The 1000 simulated mean allometry-free variability values for each group were then used to calculate confidence intervals around the actual mean variability values. Figure 1.9A shows the results of the bootstrap simulations used to compare the total dataset parsed into live and dead groups. For each shell view, the mean variability values for live and dead shells show overlapping 95% and 99% confidence intervals suggesting a high degree of similarity between the groups in terms of overall variability. In fact, the actual mean variability values for either live or dead groups (in either view) fall at least at their counterparts's 95% confidence interval.

Discussion: It is clear that the live sample represents a single cohort of individuals and thus, the variability that is shown in Figure 1.9A for the live sample can be taken as a reasonable estimate of single-generation variability. That this live variability is much the same as the variability of the death assemblage agrees well with the findings of other studies (Bell et al., 1987; MacFadden, 1989; Bush et al., 2002). The slightly higher variance of dead shells can be

explained in one of two ways. It is possible that dead shells would be more prone to have damage that would interfere with taking landmarks, such as chipping or abrasion. Such damage, if present, could elevate the variability of the dead group. However, in the replicate experiments discussed earlier, the dead shells (B102D, and C106D) had lower variances than the live shells (Table 1.3, Figure 1.4). The elevated variability of dead shells could also represent the time-averaging signature on these shells. If this is the case, then it may be that the effect of time-averaging on morphological variability is less than may have been predicted by theoretical models (see Kidwell, 1986; Bush et al., 2002).

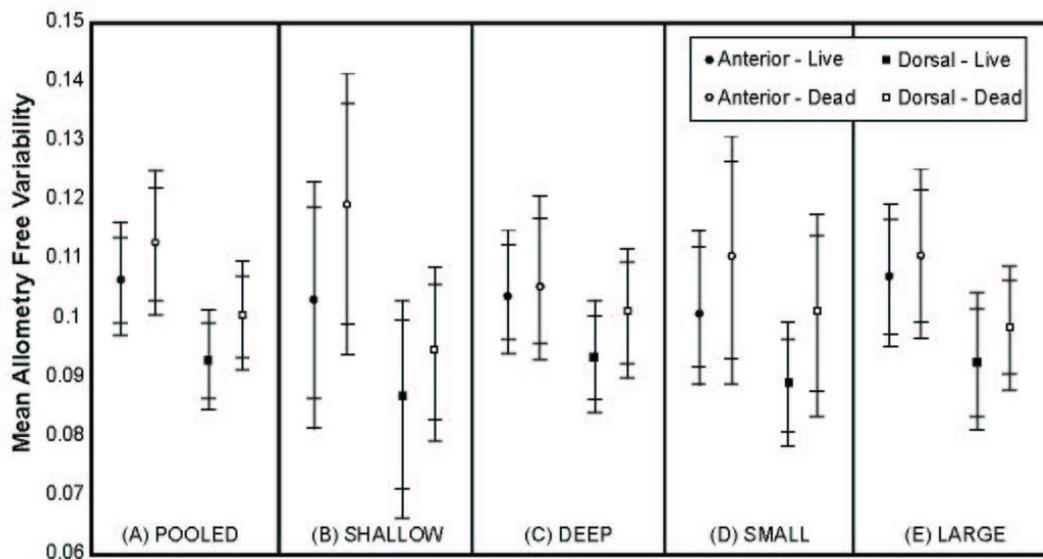


Figure 1.9 – Confidence intervals (95%, 99%) of allometry-free variability based on separate 1,000 iteration bootstraps. Live/Dead comparisons grouped by - (A) Pooled data; (B) Shallow samples (40-60m); (C) Deep samples (70-80m); (D) Small centroid size; (E) Large centroid size.

Bush et al. (2002) also found similar morphological fidelity between the life and death assemblages of the bivalves *Mercenaria campechiensis* and *M. permagana*, and presented a series of theoretical models describing the expected effects of time-averaging on shape variability in fossil assemblages (also refer to Kidwell, 1986). If the morphology of a given taxon does not change for the duration of the time averaged interval, then the fidelity of the fossil record with respect to morphology will be high. However, if shape changes during the interval of time-averaging, a number of different effects can be produced. When one considers any given morphological character that is normally distributed in the standing crop population but changes in some way during a time averaged interval, there are several ways in which the time averaged

distribution of that character can be significantly different from any given single population. For example, the central tendency of the distribution of this character can shift through time effectively increasing the morphological variance of the time-averaged assemblage. Similarly, gaps in the record can produce bimodal or multi-modal distributions of this character in the time-averaged assemblage.

From the results presented in Figure 1.9A and in Bush et al. (2002), it is clear that shape variability for *Mercenaria* and *Terebratalia* have changed very little for the duration of time-averaging of their respective assemblages. Quantitative estimates of the durations of time-averaging for molluscan assemblages have become increasingly available in the last decade (Flessa et al., 1993; Flessa and Kowalewski, 1994; Meldahl et al., 1997; Kowalewski et al., 1998). These studies dated molluscan shells (mostly *Chione fluctifraga* and *C. californiensis*) from a variety of environments ranging from beach ridges to tidal flats and channels to fan deltas in a faulted rift basin. The duration of time-averaging for these robust mollusks averaged at ~1000 years, but some environments, such as the tidal flat from Flessa et al. (1993), had averages as high as ~3000 years.

Bush et al. (2002) were able to directly compare their assemblages to those of the time-averaging studies listed above because *Mercenaria* and *Chione* are similar to each other in terms of shell form, mineralogy, and durability. However, such a comparison may not be possible for *Terebratalia* since the shell is smaller and thinner and has a different mineralogy (calcite rather than aragonite) and microstructure than *Mercenaria* or *Chione*. Furthermore, even though the calcite shell of *Terebratalia* makes it less susceptible to dissolution in modern oceans than *Mercenaria* or *Chione*, the higher organic content of the shell greatly reduces its durability shortly after the death of the organism (Daley, 1993).

Until recently, little was known about durations of time-averaging for brachiopods, probably because they do not contribute a significant amount of skeletal material to the sediment in most modern environments. An exception is the outer shelf and coastal bays of the Southeast Brazilian Bight, where recent work has documented a low-diversity, high abundance assemblage of terebratulide brachiopods that dominate that local fauna (Kowalewski et al., 2002). In a first attempt to obtain time-averaging estimates for brachiopods, Carroll and colleagues (Carroll et al., 2003; also see Barbour Wood et al., 2003), obtained dates for 82 individual shells of the most common species of the Brazilian Bight, *Bouchardia rosea*. Using amino acid racemization calibrated with AMS-radiocarbon, they found durations of time-averaging in brachiopods to be

strikingly similar (mean=460 years; standard deviation=680 years; maximum=3134 years) to those documented for mollusks (Flessa et al., 1993; Flessa and Kowalewski, 1994; Meldahl et al., 1997; Kowalewski et al., 1998). While the durations obtained for *Bouchardia* were highly variable from site to site, the results of Carroll et al. (2003) suggest that shell mineralogy and microstructure are probably not the primary factors controlling the nature and scale of time-averaging. It may therefore be reasonable to extrapolate between studies and environments to put at least a maximum estimate (≤ 3000 years) on the amount of time-averaging that the death assemblage of *T. transversa* may have experienced. The variability estimates presented here (Figs. 1.8-1.9, Table 1.4) indicate the morphological fidelity of the sub-fossil record of *T. transversa* may be rather good on centennial to millennial time scales.

Depth Comparisons

Results: It is possible that morphology or morphological variability could change between sub-groups of the dataset. The potential effect of depth on morphology may be significant, especially in light of predictions discussed earlier (Du Bois, 1916; Schumann, 1990).

Figures 1.10 and 1.11 show superimposition plots of Procrustes tangent coordinates with the dataset grouped into five depth categories corresponding to the depths sampled for this study. It should be noted that sample sizes for the 40-60m sites are rather small (Table 1.1), and it is therefore not desirable to use these categories for further analysis. However, these superimposition plots (Figs. 1.10-1.11) suggest that neither mean shape nor mean variability are substantially different among the shells from 40-60m and those from 70-80m. Therefore, grouping the dataset such that samples are parsed into 'shallow' (40-60m) and 'deep' (70-80m) groups seems most effective. All subsequent analyses for this section will be done using these groups.

The mean shapes for the shallow and deep groups were investigated in much the same manner as for the pooled, live-dead comparisons. Figures 1.5 and 1.6 show the results of PCA grouped by depth and by live-dead. The PCA plots seem to suggest a difference in mean shape between the depth groups, as defined by a difference in position of the center of one cloud of points to another. In order to rigorously test for differences between group means, CVA was run with depth groups chosen *a priori*. Figure 1.7 shows the scatter plots of CVA scores on CV1 and CV2. Separation between depth groups is somewhat better here, and indeed, the Mahalanobis

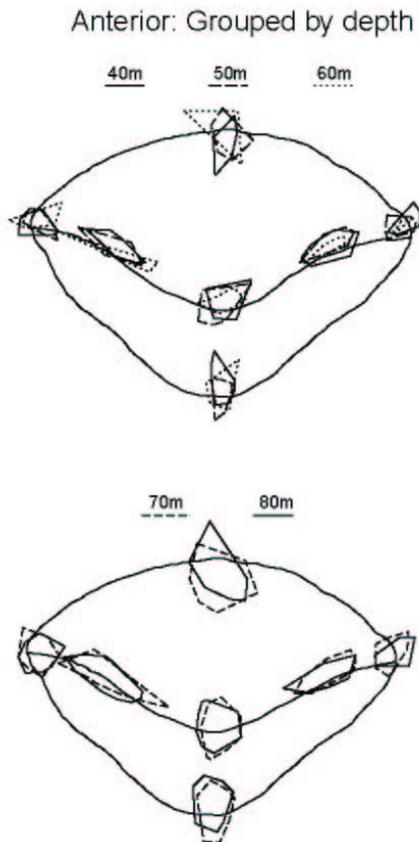


Figure 1.10 – Superimposition plots of procrustes tangent coordinates for anterior view grouped by five depths, for both views. (A) Anterior view, 40-60m. (B) Dorsal view, 40-60m. (C) Anterior view, 70-80m. (D) Dorsal view, 70-80m.

distances derived from the CVA do indicate significant differences between at least some of the depth groups, especially in the anterior view (Table 1.5). However, as indicated earlier for the pooled live-dead comparisons, there is still a substantial amount of overlap between the depth groups in ordination space for both views. Additionally, the Mahalanobis distances do not agree between shell views - distances for the anterior view are nearly all significant while those derived from the dorsal view data are not. This disagreement among shell views suggests that distinguishing between uniform and non-uniform shape change and/or utilizing a 3D geometric morphometric analysis may be necessary to draw conclusions about mean shape changes with depth for *Terebratalia transversa*, both of which are beyond the scope of the present study.

Figures 1.12 and 1.13 show superimposition plots of Procrustes tangent coordinates for anterior and dorsal views, respectively, with groupings of shallow (40-60m) and deep (70-80m) as well as live and dead categories. The results of the live-dead comparison grouped by depth

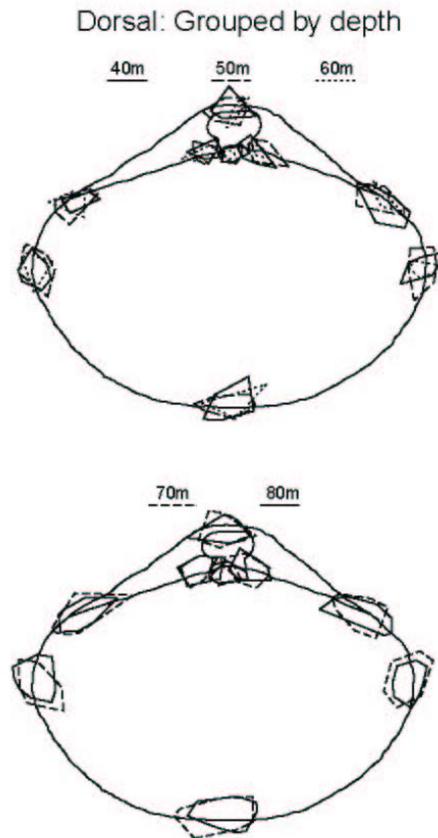


Figure 1.11 - Superimposition plots of procrustes tangent coordinates for dorsal view grouped by five depths, for both views. (A) Anterior view, 40-60m. (B) Dorsal view, 40-60m. (C) Anterior view, 70-80m. (D) Dorsal view, 70-80m.

roughly mirror those of the pooled data (Fig. 1.8, 1.9B, C). No distinct morphogroups, live or dead, can be recognized at different depths for either shell view. As in other analyses, dead shells seem to be somewhat more variable than live, but this difference is negligible as mean allometry-free variability values have substantially overlapping bootstrapped confidence intervals for both shallow and deep groups and both views (Fig. 1.9B, C). It is interesting to note that Figure 1.9B shows rather large confidence intervals for the shallow group of the dataset, and it is tempting to interpret this result as a change in shape variability with depth. However, even after grouping depths together to run these analyses, the shallow sample is still substantially smaller than that for the deep group (Table 1.1). Thus, while these data may indicate a decrease in shape variability with increasing depth for *Terebratalia transversa*, the difference in sample size for the two depth groups does not allow rejection of the null hypothesis of similarity.

Anterior: live/dead grouped by depth

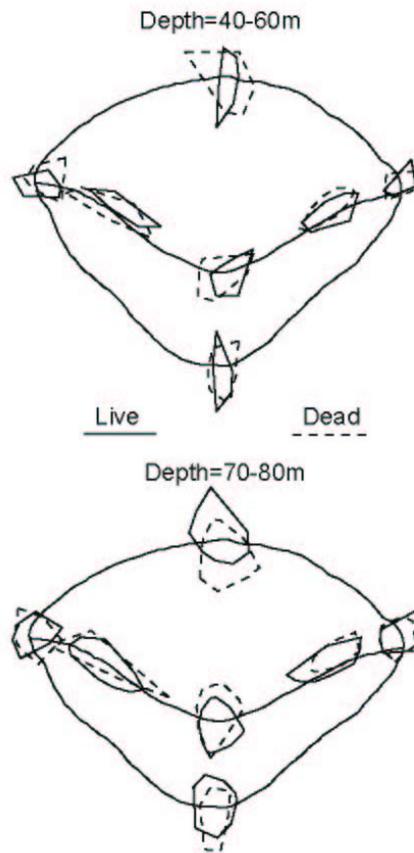


Figure 1.12 - Superimposition plots of procrustes tangent coordinates for anterior view, showing comparison of Live/Dead grouped by depth. (A) Anterior view, 40-60m. (B) Dorsal view, 40-60m.

Discussion: Regardless of whether overall shape variability changes with depth, it is clear that live and dead specimens from any given depth category have a very similar magnitude of variability. Therefore, one can deduce that the fidelity of morphological disparity within *Terebratalia transversa* is very good at any depth, as long as large-scale spatial mixing of assemblages can be ruled out. While no evidence for such mixing was encountered during this study (also see Kowalewski et al., 2003), it was not explicitly addressed.

Size Comparisons

Results: As mentioned earlier, *Terebratalia transversa* exhibits a slight allometry with growth. Schumann (1990) noted this when he was delineating his morphotypes. Juvenile *T. transversa* are, in general, more alate and less inflated, with less prominent sulci, a form which

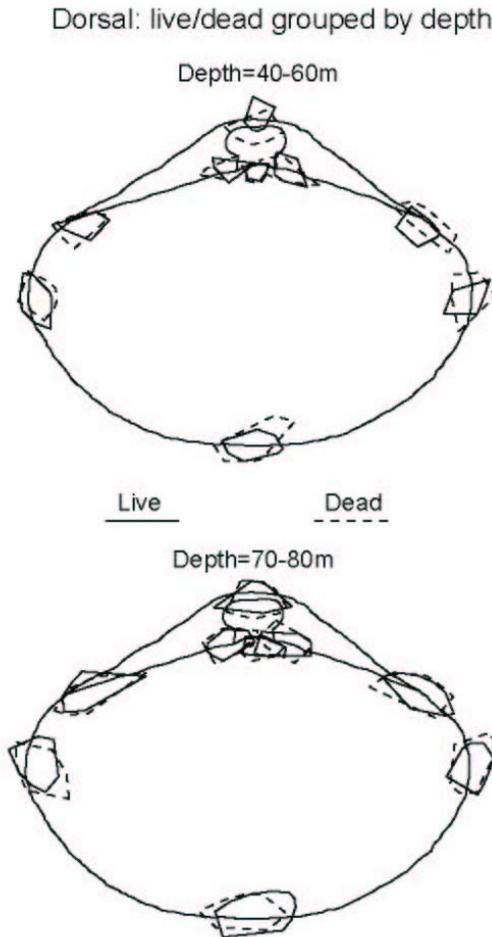


Figure 1.13 - Superimposition plots of procrustes tangent coordinates for dorsal view, showing comparison of Live/Dead grouped by depth. (A) Anterior view, 40-60m. (B) Dorsal view, 40-60m.

roughly corresponds to the ‘Spirifer’ morphotype. In order to mount an exhaustive search for morphogroups or changes in morphology one must be aware of allometric growth, but a full treatment of the allometry of *T. transversa* is beyond the scope of this paper. This subject has been dealt with elsewhere albeit outside of a geometric morphometric framework (Paine, 1969; Thayer, 1977; Rosenberg et al., 1988).

Size was categorized using centroid size derived from Procrustes analysis. Each set of landmarks yielded a unique centroid size for each shell, thus each particular shell had two centroid sizes. Obviously these two measures are highly correlated for both live and dead shells ($r^2_{\text{Live}}=0.990$, $r^2_{\text{Dead}}=0.970$) although anterior centroid size was consistently slightly smaller than dorsal centroid size (Fig. 1.14). The size categories used (small and large) were calculated by taking the median centroid size for each view. ‘Small’ shells were considered to have a centroid

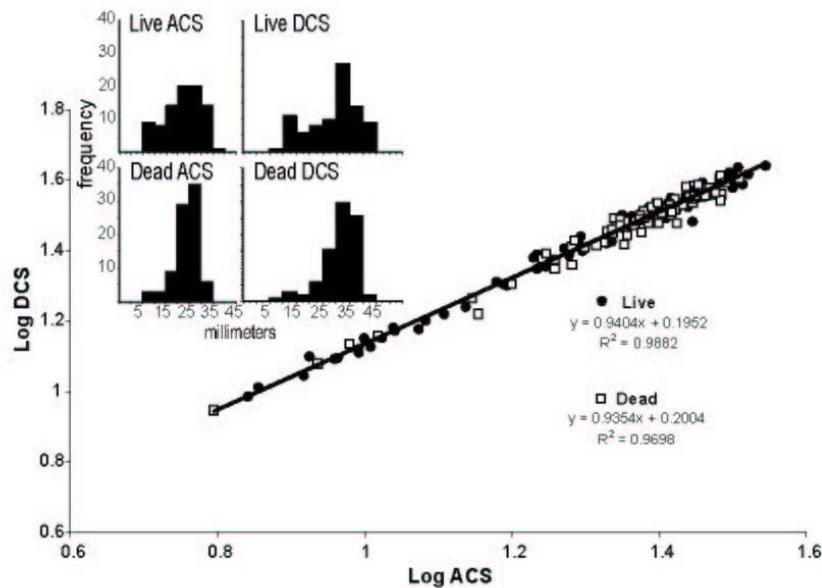


Figure 1.14 - Comparison of centroid sizes from both views. (A) Bivariate scatterplot showing linear relationship between log dorsal centroid size (DCS) and log anterior centroid size (ACS). (B) Centroid size-frequency distributions.

size smaller than the median, while ‘large’ shells had a centroid size larger than the median (the shell of median size was arbitrarily placed in the ‘large’ group for each view). Because each shell had two size measures, and because they were not identical for any given shell, some shells were assigned to the ‘large’ category for the anterior centroid size, but to the ‘small’ category for dorsal centroid size, and vice versa. This is why sample sizes are different between the two large and the two small groups (Table 1.4). In order to be able to draw meaningful size comparisons between the live and dead shells used in the study, the size-frequency distributions (Fig. 1.14) of each of the centroid sizes had to be investigated. Each of these distributions shows a left-skewed distribution, a rather unusual distribution for biological populations which are generally right-skewed. This is a result of a sampling bias, present because very small shells would not yield useable images that were conducive to taking landmarks. Importantly, the shapes of the live and dead size-frequency distributions for both views are not significantly different (Kolmogorov-Smirnov Test: $p_{\text{Dorsal}}=0.07$; $p_{\text{Anterior}}=0.07$), nor are their central tendencies (Kruskal-Wallis Test: $\chi^2_{\text{Dorsal}}=1.53$, $p=0.22$; $\chi^2_{\text{Anterior}}=1.79$, $p=0.18$) making comparisons between them reasonable (Fig. 1.14).

An analysis of mean shapes for size groups was also conducted, but the results are again ambiguous as they were for depth groups. Figures 1.5, 1.6, and 1.7 show the results of PCA and CVA respectively for the dataset grouped into small and large categories. Again, a test of

significance for the Mahalanobis distances derived from CVA does not yield clear results (Table 1.5). Both CVA and PCA show substantial overlap between groups in ordination space and this variability may override the significant differences in mean shape between the groups.

Figure 1.15 shows the results of Procrustes analysis of landmarks from both views, grouped by centroid size. The allometry mentioned earlier, and noted by Schumann (1990) is easily seen. Small shells are wider, shorter, and less inflated than large shells which are

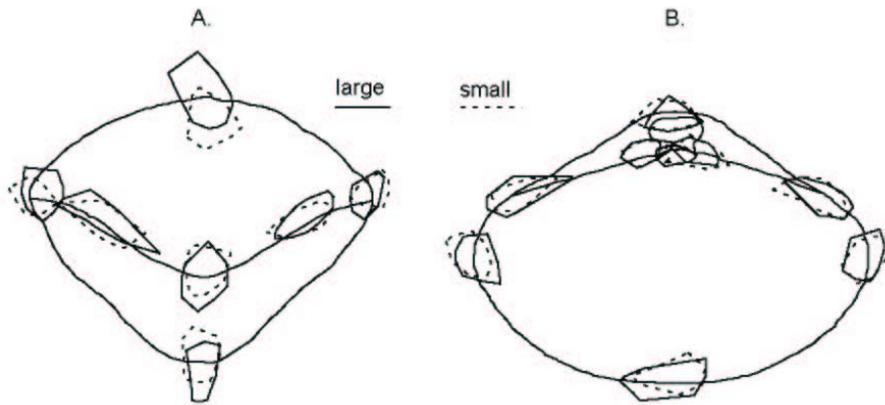


Figure 1.15 - Superimposition plots of procrustes tangent coordinates of both views showing a comparison of centroid size categories. (A) Anterior view. (B) Dorsal view.

generally more globose. Figures 1.16 and 1.17 show the results from Procrustes analysis with live-dead and size groups separated out. As was noted previously for other groupings of the data, live and dead groups overlap substantially on these superimposition plots, and there is no indication of distinct morphogroups for either view. Furthermore, mean allometry-free variability values (Fig. 1.9D, E) are, again, very similar with a large degree of overlap in confidence intervals for each pairwise (live-dead) comparison.

Discussion: Schumann (1990) postulated that all juvenile shells of *Terebratalia transversa* have a shape similar to the ‘Spirifer’ morphotype, and that, as each individual grows, its morphology usually diverges from that form in one of several different ways, in response to environmental factors. While this study did not include juvenile shells, the results presented in the previous section seem to be inconsistent with that hypothesis. The shape variability of *T. transversa* is a trait that is present with the same magnitude in both small and large shells (Fig. 1.9D, E), and thus it is not likely to be a trait that changes during ontogeny. The implication is that assemblages of small individuals should be just as morphologically variable as assemblages of large individuals.

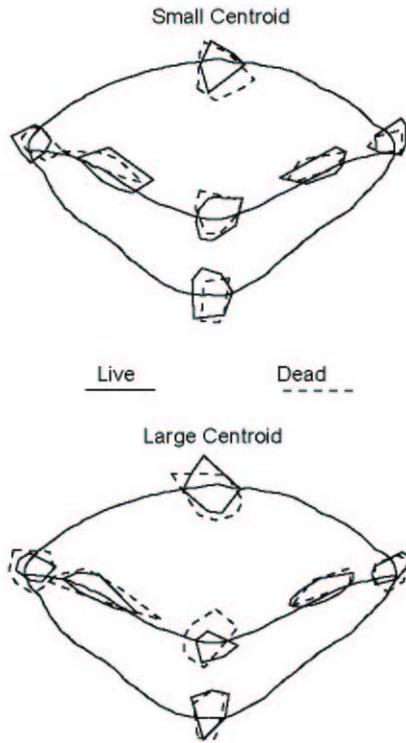


Figure 1.16 - Superimposition plots of procrustes tangent coordinates for anterior view showing a comparison of live/dead grouped by size.

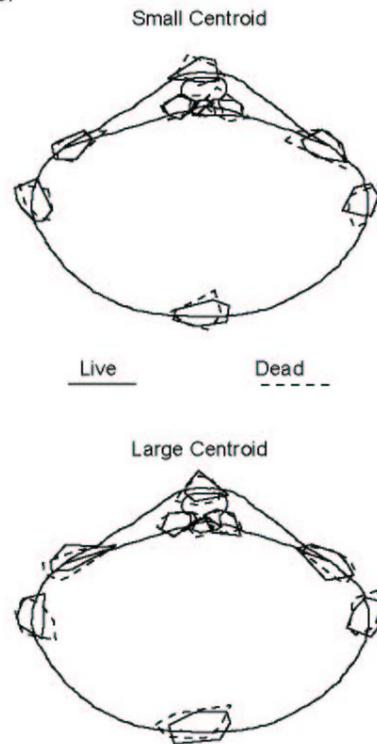


Figure 1.17 - Superimposition plots of procrustes tangent coordinates for dorsal view showing a comparison of live/dead grouped by size.

CONCLUSIONS

The shape variability of the terebratulide brachiopod *Terebratalia transversa* is remarkably consistent in life and death assemblages. This trend persists when all data are pooled, when individuals are grouped by depth, and when individuals are grouped by size. Change in average shape between groups is more ambiguous, and often cannot be separated from the shape variability of the groups in question. Additionally, this study found no evidence of distinct morphogroups in populations of *T. transversa*. Rather, variability seems to be continuous from one form to another. Furthermore, the range of variability is remarkably similar at all sites sampled, which encompass the entire depth range of the species in the area, and for different size groups.

Given the similar range of morphological variability at each site, it is possible that the wide array of micro-environments available at any given place in the San Juan Channel (exposed or cryptic, high or low current depending on orientation of cobble substrate), could exert a strong control on the morphology of *Terebratalia transversa*. This control could work in concert with the species' apparent inability to reorient itself under changing conditions (Thayer, 1975, 1977; LaBarbera, 1977) to produce the high degree of variability observed at each site. This is similar to Schumann's (1990) suggestion discussed earlier, but since a wide range of micro-environments is probably available at any given site, populations from each site exhibit a similar amount of morphological variance.

The consistency in morphological variability between the living population and its sub-fossil record is documented here for the first time in brachiopods, and has important implications for the fossil record of the group. It appears that morphological variance of the standing crop population can be estimated from that population's death assemblage, even in organisms whose shells break down quickly after death (Daley, 1993). This also means that the brachiopod fossil record may be relatively complete with respect to morphological variants of all of the constituent species. The recognition of morphologically variable species, as such, may in that case be possible in the fossil record, especially by utilizing the powerful geometric morphometric techniques employed herein.

CHAPTER TWO¹: Body size estimates from the literature: Utility and potential for macroevolutionary studies

¹ This paper was submitted for publication to *Palaios* on 7 November 2005. The co-authors for this publication, Jennifer A. Stempien, Michał Kowalewski, and Arnold I. Miller, contributed less than 20% to the data collection and analysis stages of this project. The text was written completely by R.A. Krause.

ABSTRACT

Images in the monographic literature represent an important but relatively untapped, resource for paleontologists. In particular, they could provide vast amounts of body size data. However, it is possible that images of specimens represent a biased sample of the fossil record. Thus, before body size estimates from the literature can be used in analyses, the quality of these data must be assessed.

Two complementary datasets were constructed for a group of bivalve and brachiopod species from the Paleozoic and the Cenozoic. The monograph dataset consisted of length measurements taken from all unique images of a species in a monograph. The counterpart bulk dataset consisted of comparable measurements taken from a set ($n > 10$) of bulk-collected specimens of the same species, acquired from the same locality, as those figured in the monograph. These paired datasets for each species were used to assess the quality of monographic data.

Bias direction and magnitude were assessed by using the bulk sample of a species as an estimate of its underlying size-frequency distribution. Bias was estimated for each monographed specimen by calculating its percentile-value in relation to the size-frequency distribution for that species. All species groups had mean values within the 70th to 85th percentile range, indicating a significant bias toward monograph specimens that are larger than the mean of the bulk sample. The consistency of bias was evaluated by comparing the monograph sample mean to the bulk sample mean for each species. When compared in bivariate scatter plots, all species groups yielded significant regression lines with slopes near unity, indicating highly consistent, yet predictable, bias in each case. This trend persisted when the data were grouped taxonomically, geographically, or by year of monograph publication.

These results indicate that size measurements of monographed specimens of bivalves and brachiopods consistently record similar size-classes for most species. This bias is easy to remove, and doing so renders size data from images in monographs useful for macroevolutionary studies of body size.

INTRODUCTION

Images of specimens are essential to the taxonomic literature. They enable an author to concisely present descriptive and comparative information on specimens, which cannot be easily expressed in words (Mayr et al., 1953). Images also remove an element of subjectivity from the description of species – allowing the reader to see the specimen that is being described. For this reason, it is not uncommon for taxonomic journals to require high-quality images to accompany any description of a new species, and images are highly encouraged in papers not focusing on alpha-taxonomy as well (Journal of Paleontology, Instructions for Authors, <http://www.journalofpaleontology.org/instruct.htm>). In fact, many taxonomic publications include numerous images in order to fully document the natural variability of a population. As a result, published images afford a researcher the opportunity to view a representative suite of specimens from any species, in collections from all over the world.

Despite their central importance in alpha taxonomy, published images of specimens have been underutilized by paleontologists engaged in the analysis and synthesis of existing taxonomic information. In the last few decades, these workers have established themselves as a fundamental enterprise of modern paleontology (Adrain, 2001), by drawing heavily on the taxonomic literature to examine large-scale patterns in the history of life. Yet the types of data extracted from the literature have remained rather limited. Most often, biodiversity studies (Newell, 1959; Valentine, 1969; Sepkoski, 1982; Sepkoski, 1992; Benton, 1993; Sepkoski, 2002) have utilized taxon names and ranges compiled from numerous publications. Other studies have used taxon occurrences in fossil collections (Alroy et al., 2001), species richness at single localities (Bambach, 1977), and relative abundance in bulk-collected samples (Powell and Kowalewski, 2002). The full scope of data types in the taxonomic literature are just beginning to be explored in large, community-wide initiatives such as the Paleobiology Database (<http://paleodb.org>). Yet, the images in taxonomic publications remain as untapped resources with great potential.

Such images could be used as a primary or supplementary data source in many types of studies that have traditionally been considered “specimen-based”. For example, because taxonomists take great care to visually document all diagnostic features of a species, published images can yield a wealth of morphological information, from simple linear dimensions to landmark coordinates for geometric morphometric analysis.

The inclusion of image-derived data in a study is advantageous to the researcher in several ways. Images in monographs allow quick examination of large numbers of specimens that have been taxonomically identified by an expert on that group. These specimens may be repositied in museum collections that are geographically remote or otherwise difficult to access, but their images can be studied in any major university library. In addition, these images are often tied directly to detailed information on locality and sampling horizon (Kowalewski, 2002) that closely approximates the level of detail commonly available in a museum or field collection.

Despite their promise, data derived from images may be biased in several ways, depending on the type of information being extracted. The purpose of the present paper is to investigate the biases inherent in the collection of simple linear measurements from published images. Specifically, the quality of these data will be assessed with respect to three parameters: (1) bias direction – the presence of non-random departures from the actual mean size of a species; (2) bias magnitude – the absolute value of the mean departure, that is, the imprecision of the data; and (3) bias consistency – the variation in the direction and magnitude of bias within and across monographs, higher taxa, or time intervals. Only with a clear understanding of these bias parameters will it be possible to assess the utility of monograph-derived size data.

TYPES OF PHOTOGRAPHIC BIAS

Apparent Versus Actual Size

One potential problem with photographs is that they may not accurately reproduce the sizes of the specimens. Distortions can occur at many stages of the photographic process, including improper orientation of a specimen or camera, poor lighting, or a failure to accurately report magnification.

While it is difficult to address each of these problems in isolation, several studies have addressed this issue by studying the concordance of measurements of specimens and their images. Kowalewski and colleagues (2000) studied predatory drill hole size in Permian brachiopods and showed that photographic distortion introduces negligible error even when measuring items less than a millimeter in diameter. Similar studies have been conducted on grain size distributions in coarse sediment samples (Ibbeken and Schleyer, 1986; McEwan et al., 2000; Butler et al., 2001; Sime and Ferguson, 2003). These studies found a significant difference between grain size distributions taken from photographs and those taken from direct grain measurement of the same sample. Fortunately, image-derived grain size distributions always deviate from traditionally collected grain size distributions in a predictable way – distributions derived from images are always too fine by some amount, (this is because shadows cast on grain boundaries make all grains appear smaller in images than they actually are). The magnitude of this bias is invariant across a range of environments and thus, can be easily corrected (Sime and Ferguson, 2003).

Sampling Bias

In addition to the disparity between the apparent versus actual size of an object, there is another issue to consider: the potential for bias introduced by the choice of specimens photographed by the author of a monograph.

The author's choice of specimens to photograph may be a biased sample with respect to size. This can be purely accidental, perhaps caused by an unconscious tendency to pick certain size classes over others, or a deliberate attempt to illustrate certain size classes that display specific morphological features. In this study the latter possibility has been controlled for, by excluding monographs that intend to study size relationships in a population, such as ontogenetic series. Thus, it is the potential worker-induced bias that is under scrutiny here. Such a bias, if

present, can lead to serious problems for the researcher interested in extracting meaningful size data from the monographic literature.

TABLE 2.1 - Attributes of the bulk sample and monograph sample for each species. Bulk sample: n_{bulk} is the number of specimens measured by us, or the author of the monograph; n_{total} is the total number of specimens that were available from a particular sample, when unreported, this category is scored as "-". Monograph sample: n_{mon} is the number of measured monograph specimens for each species. Abbreviations: O - Ordovician; S - Silurian; D - Devonian; M - Mississippian; P - Paleocene; E - Eocene; Mio. - Miocene; Plio. - Pliocene; R - Recent. References: 1=Alberstadt, 1979; 2=Amano, 1986; 3=Amsden, 1968; 4=Babin & Melou, 1972; 5=Balinski, 1995; 6=Balinski, 1997; 7=Bird, 1965; 8=Cooper, 1988; 9=Craig, 2000; 10=Gordon et al., 1993; 11=Howe, 1979; 12=Johnston, 1993; 13=Jung, 1996; 14=Lauriat-Rage, 1982; 15=Li & Jones, 2003; 16=Liljedahl, 1983; 17=Liljedahl, 1984; 18=Pope, 1982; 19=Sanchez, 1986; 20=Sanchez, 1990; 21=Sanchez et al., 1995; 22=Soot-Ryen, 1964.

Brachiopods							Bivalves						
species	n_{mon}	n_{bulk}	n_{total}	period	ref.	region	species	n_{mon}	n_{bulk}	n_{total}	period	ref.	region
<i>Adaria adairensis</i>	2	24	117	M	10	Ozark region, USA	<i>Anadara transversa</i>	2	54	-	Mo.	7	Natural Well, NC, USA
<i>Antiirhynchonella thomasi</i>	9	29	200	S	3	Ozark region, USA	<i>Anadara transversa</i>	1	20	-	Plio.	7	Town Creek, NC, USA
<i>Athyra erugata</i>	5	19	50	S	3	Ozark region, USA	<i>Anadara transversa</i>	1	20	-	Plio.	7	James City, NC, USA
<i>Basiliola</i> sp.	3	15	-	P	9	Camaron Basin, w. Australia	<i>Astarte fusca incrassata</i>	6	50	-	Plio.	14	St. Michel, Pays de la Loire, France
<i>Biernatella lentiformis</i>	7	103	-	D	5	Holy Cross Mtns., Poland	<i>Astarte ornalii ornalii</i>	21	29	-	Plio.	14	Nantes, Pays de la Loire, France
<i>Biernatella ovalis</i>	4	15	-	D	5	Holy Cross Mtns., Poland	<i>Astarte ornalii scalaris</i>	25	176	-	Plio.	14	Nantes, Pays de la Loire, France
<i>Biernatella polonica</i>	1	26	-	D	5	Holy Cross Mtns., Poland	<i>Astarte ornalii scalaris</i>	33	128	-	Plio.	14	Angers, Pays de la Loire, France
<i>Dicarracopsis parva</i>	13	93	200	S	3	ARand OK, USA	<i>Astarte solidula</i>	5	100	-	Plio.	14	Nantes, Pays de la Loire, France
<i>Dicelcosia bilobella</i>	5	33	100	S	3	ARand OK, USA	<i>Astarte sulcata rednensis</i>	4	50	-	Plio.	14	St. Michel, Pays de la Loire, France
<i>Dicelcosia oklahomensis</i>	3	13	-	S	3	ARand OK, USA	<i>Astarte sulcata rednensis</i>	1	51	-	Plio.	14	le Houx, Pays de la Loire, France
<i>Eospirifer acutolineatus acutolineatus</i>	5	29	100	S	3	ARand OK, USA	<i>Cadornia typa</i>	2	16	16	O	19	western Argentina
<i>Eospirifer acutolineatus pentagonus</i>	6	30	300	S	3	ARand OK, USA	<i>Cardomya (C.) islahispanidae</i>	6	25	-	Mo.	13	Dominican Republic
<i>Giraliathyris kaitirinae</i>	2	54	-	P	9	Camaron Basin, w. Australia	<i>Cardomya (Bowdenia) distra</i>	4	28	-	Mo-	13	Dominican Republic
<i>Giraliathyris jubileensis</i>	3	44	-	E	9	Camaron Basin, w. Australia	<i>Cornelites catellus</i>	1	14	34	D	12	southeastern Australia
<i>Giraliathyris monamara</i>	1	81	-	P	9	Camaron Basin, w. Australia	<i>Crassatellopsis lenticularis</i>	8	15	15	D	12	southeastern Australia
<i>Hirinisca haviocski</i>	4	22	45	S	3	ARand OK, USA	<i>Opricardina minima</i>	3	18	18	D	12	southeastern Australia
<i>Inflatia cherokeensis</i>	2	48	100	M	10	Ozark region, USA	<i>Digitaria digitaria</i>	2	68	-	Plio.	14	le Pigeon-Blanc, Pays de la Loire, France
<i>Inflatia dydensis</i>	2	12	102	M	10	Ozark region, USA	<i>Digitaria digitaria</i>	1	38	-	Plio.	14	la Gauviniere, Pays de la Loire, France
<i>Inflatia cooperi</i>	2	15	42	M	10	Ozark region, USA	<i>Eoschizodus taemasensis</i>	2	14	18	D	12	southeastern Australia
<i>Inflatia gracilis</i>	1	12	32	M	10	Ozark region, USA	<i>Freja fecunda</i>	3	65	164	S	17	Gotland, Sweden
<i>Inflatia inflata</i>	2	27	40	M	10	Ozark region, USA	<i>Glycymeris americana</i>	3	40	-	Plio	7	Old Dock, NC, USA
<i>Inflatia pusilla</i>	1	24	165	M	10	Ozark region, USA	<i>Glycymeris anteparilis</i>	2	21	-	Mo	7	Silverdale, NC, USA
<i>Kozłowskiella (K.) vaningeri</i>	6	47	200	S	3	ARand OK, USA	<i>Glycymeris icidensis</i>	3	50	-	Mo.	2	Hokkaido, Japan
<i>Mertisina clarensis</i>	3	21	60	S	3	ARand OK, USA	<i>Glycymeris pectinata</i>	2	20	-	Plio	7	Acme, NC, USA
<i>Nanospira clarensis</i>	11	67	200	S	3	ARand OK, USA	<i>Glycymeris subovata</i>	2	21	-	Mo	7	James River, VA, USA
<i>Nucleospira lens</i>	1	36	645	D	15	Arctic Canada	<i>Goniophora duplisulca</i>	3	27	29	D	12	southeastern Australia
<i>Oepikina mimesotensis</i>	26	80	-	O	18	northern KY, USA	<i>Gotobonta gotlandica</i>	4	62	214	S	22	Gotland, Sweden
<i>Oepikina mimesotensis</i>	13	94	-	O	18	northern KY, USA	<i>Haliotis jarraicensis</i>	3	10	-	Plio.	13	Dominican Republic
<i>Othorhynchula limneyi</i>	3	38	-	O	11	northern KY, USA	<i>Janeia silurica</i>	3	18	597	S	17	Gotland, Sweden
<i>Othorhynchula sublimneyi</i>	7	39	-	O	11	northern KY, USA	<i>Madicolopsis cuyana</i>	1	17	17	O	20	western Argentina
<i>Plonomera recens</i>	10	65	-	O	18	northern KY, USA	<i>Mycoplusia contrastans</i>	4	17	35	O	4	Orozon, France
<i>Platystrophia annieana</i>	4	33	-	O	1	northern KY, USA	<i>Mytilarca bloomfieldensis</i>	6	13	18	D	12	southeastern Australia
<i>Platystrophia calbiensis</i>	4	14	-	O	1	northern KY, USA	<i>Nobelia (Eontia) carolinensis</i>	1	20	-	Mo	7	Black Rock, NC, USA
<i>Platystrophia elegantula</i>	1	10	-	O	1	northern KY, USA	<i>Nobelia (Eontia) limula</i>	1	20	-	Plio	7	James City, NC, USA
<i>Platystrophia ponderosa</i>	7	34	-	O	1	northern KY, USA	<i>Nobelia (Eontia) platyura</i>	1	20	-	Plio	7	Town Creek, NC, USA
<i>Plicatoria wilingtonensis</i>	25	80	251	E	8	Wilmington, NC, USA	<i>Nobelia (Eontia) trigintinaria</i>	2	16	-	Mo	7	Natural Well, NC, USA
<i>Plicatoria wilingtonensis</i>	8	235	235	E	8	Wilmington, NC, USA	<i>Nuculites argentinum</i>	7	19	25	S	21	western Argentina
<i>Rhynchotrema increbescens</i>	7	29	-	O	11	northern KY, USA	<i>Nuculodonta gotlandica</i>	6	197	218	S	16	Gotland, Sweden
<i>Soverbyella</i> sp.	5	23	-	O	11	northern KY, USA	<i>Nuculoida lens</i>	6	142	153	S	16	Gotland, Sweden
<i>Terebratulina lachryma</i>	1	24	24	E	8	SC, USA	<i>Plectodonta granulatus</i>	4	20	-	R	13	Caribbean Sea
<i>Terebratulina wilsoni</i>	2	48	48	E	8	SC, USA	<i>Similodonta djupvikensis</i>	1	15	26	S	22	Gotland, Sweden
<i>Victorithyris bleakerum</i>	4	39	-	P	9	Camaron Basin, w. Australia	<i>Trigonulina bowdenensis</i>	8	54	-	Mo-	13	Dominican Republic
<i>Victorithyris decapello</i>	2	54	-	P	9	Camaron Basin, w. Australia	<i>Trigonulina ornata</i>	4	74	-	R	13	Caribbean Sea
<i>Waidhya sulcairina</i>	3	31	-	D	6	Holy Cross Mtns., Poland	<i>Trigonulina pacifica</i>	5	155	-	R	13	Santa Catalina Island, CA, USA

METHODS

To test for size bias in the monographic literature, this study focuses on 39 bivalve and 42 brachiopod species. The few species with data from more than one locality were treated separately, resulting in 88 discrete species-localities (44 bivalve, 44 brachiopod) distributed among 22 monographs (Table 2.1). For simplicity, each discrete species-locality will hereafter be referred to as a species. Monographs are defined in this study as any publication that deals primarily with alpha taxonomy or faunal description, and includes high-quality images of specimens. This definition of monographs includes what others have referred to as synopses and reviews, revisions, and faunal works, as well as monographs *sensu stricto* (Mayr et al., 1953).

Material from both the Paleozoic and Cenozoic were used to assess the possibility of temporal variations in monographic bias. However, in most cases, the monographs used did not overlap in their temporal coverage. As a result, the main grouping of the data was a Paleozoic and Cenozoic sample for each clade. For brachiopods, Ordovician through Mississippian specimens were placed into the Paleozoic group and Paleocene and Eocene specimens were placed into the Cenozoic group. For bivalves, Ordovician through Devonian specimens were placed into the Paleozoic group while Miocene, Pliocene, and Recent specimens were placed in the Cenozoic group.

To investigate the effect of other factors on monographic bias, several other grouping variables were used. We conducted separate analyses using geographic origin, year of monograph publication, and total sample size available to an author as grouping variables. Each of these potential confounding factors, and their effects on monographic bias, will be explained in more detail below.

In this study we use a single length measurement as a proxy for size of each specimen. This is a reasonable procedure because length is highly correlated with other size measures such as body mass and diameter in most organisms (Niklas 1994). For brachiopods, length is defined as the maximum distance from the hinge to the commissure. For bivalves, length is defined as the maximum distance from the umbo to the commissure that is perpendicular to the hinge axis.

For each species, two parallel samples were generated. The monograph sample consisted of length measurements taken from photographs of specimens in monographs. A total of 449 monographed specimens from the 88 species of bivalve and brachiopod were analyzed (Table 2.1). The counterpart, or bulk sample, consisted of length and width measurements taken from

88 bulk-collected samples, one for each of the species. Each bulk sample consisted of at least 10 specimens and was always from the same locality or region as the specimens for that species measured in the monograph. All of the bulk samples used in this study came from tables or plots of raw measurements reported in the publications used to construct the monograph sample. Thus, the monograph and bulk samples are directly comparable because they were drawn from the same underlying population of a species at a locality.

All statistical analyses were performed with codes written by MK and RAK in SAS and SAS/IML version 9.1. A significance criterion of 5% ($\alpha = 0.05$) was used for the determination of statistical significance.

Specimen-Level Analysis

Size frequency distributions were constructed for each species from their bulk samples (Fig. 2.1A). The percentile value of each monograph measurement for a species was then defined by comparing it directly to the size-frequency distribution of the bulk sample (Fig. 2.1A). The result was a dataset consisting of size-standardized monograph measurements expressed as percentiles of underlying population distributions.

Percentiles were then grouped into percentile-frequency distributions to determine both the magnitude and the direction of bias in the monograph sample (Fig. 2.1B). For example, a percentile-frequency histogram with a mean near the 50th percentile would indicate that the monograph data for that group of species, when considered as a whole, are not biased with respect to their bulk samples. However, if the percentile-frequency plots are shifted significantly to the right or left, monograph data are smaller or larger, respectively, than the majority of bulk sample specimens.

Species-Level Analysis

To investigate monographic bias at the species level, the average size of all monographed specimens for each species was computed. This value was then compared to the average size from each species' bulk sample (Fig. 2.1C). Specific groups of species were then compared through a series of simple scatter plots (Fig. 2.1D).

Figure 2.2 depicts a series of null-models for this analysis. In the best-case scenario (Fig. 2.2A), the average size of specimens in monographs is nearly the same as the average size of specimens in the bulk sample, resulting in a group of points whose regression line has a slope of

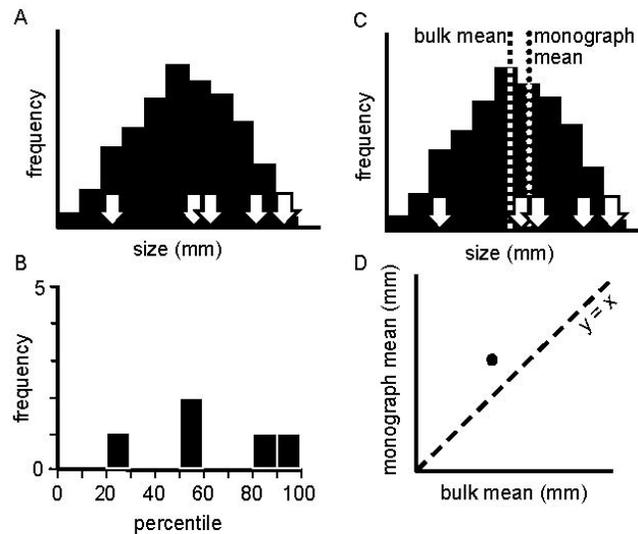


Figure 2.1 - Construction of the datasets. (A) A size-frequency distribution is constructed for each species from measurements taken from specimens in the bulk sample. Measurements of images of these specimens from monographs are then compared to these size-frequency distributions (white arrows). (B) Specimen-level analysis: Each monograph image is assigned a percentile value in relation to its bulk size-frequency distribution. Percentile-frequency distributions are then constructed for groups of species. (C) Species-level analysis: The mean of the bulk size-frequency distribution for a species is compared to the mean size of monographed specimens for that species with simple scatter plots.

unity and lies along the line of equality. This scenario would essentially demonstrate a lack of monographic bias, with respect to size, for this group of species.

A somewhat less ideal case is illustrated in Figure 2.2B. Here, monographed specimens show a slight size-bias with respect to the average size of bulk sample specimens. However, the magnitude of the size bias is consistent from species to species, regardless of size, resulting in a grouping of points whose regression line has a slope of unity but does not lie on the line of equality. In this scenario, size measurements from photographs in monographs would still be useful because the bias is consistent and easily corrected for all species across a wide size range.

A third model, shown in Figure 2.2C, illustrates a scenario where monographs are a highly imprecise predictor of the average size of bulk sample specimens. This results in a cloud of points with a regression line that fits the data poorly (low R^2 value) and may or may not have a slope near unity or lie along the line of equality. Monograph data fitting this model would not serve as a useful proxy for actual temporal size trends because the monographic bias is not consistent for all species used in the analysis.

A fourth model, shown in Figure 2.2D, depicts a scenario in which monograph data are not only imprecise predictors of the average size of the bulk sample specimens, but are also

inconsistent, in that the magnitude of the bias is highly variable from species to species. Clearly, monograph data falling into this category would be wholly unusable as a proxy for size of the original population.

A final scenario is illustrated in Figure 2.2E. It is possible that the size of monographed specimens could vary linearly, or in some more complex fashion, with the mean sizes of the bulk samples. A situation like this could arise from researchers always choosing the same size class of specimens to photograph, regardless of the size distribution of the population. Such a scenario may also render monograph data useless.

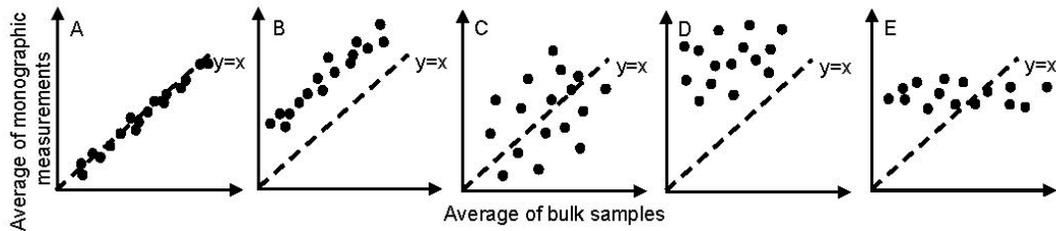


Figure 2.2 - Null models for species-level analysis. (A) Images in monographs are not biased with respect to the bulk sample. (B) Images in monographs are biased, but the magnitude of the bias is similar for all species across a wide size range. (C) Some species exhibit a monographic size bias, others do not. Magnitude of bias is not consistent across species. (D) All species exhibit a monographic size bias, but its magnitude is not consistent across species. (E) Size of specimens in monographs is invariant across a wide size range. Magnitude of bias is not consistent across species.

RESULTS

Specimen-Level Analysis

The percentile-frequency distributions in Figure 2.3 summarize the results from the specimen-level analysis. Each group of the data displays a markedly left-skewed distribution, which indicates that the majority of monograph images in each group have sizes that fall well above the 50th percentile for a given species' bulk-collected size-frequency distribution. In fact, the means of these distributions are tightly constrained between the 65th and 69th percentile (Fig. 2.4; Table 2.2, 1st group). Statistical comparisons of the distributions show no significant difference in central tendency or distribution shape (Table 2.3).

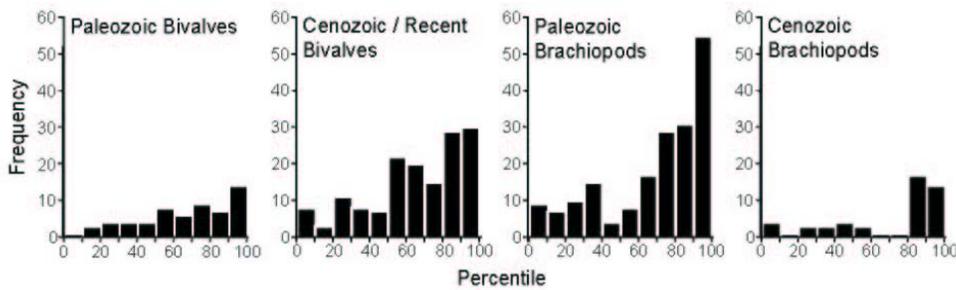


Figure 2.3 - Percentile-frequency distributions.

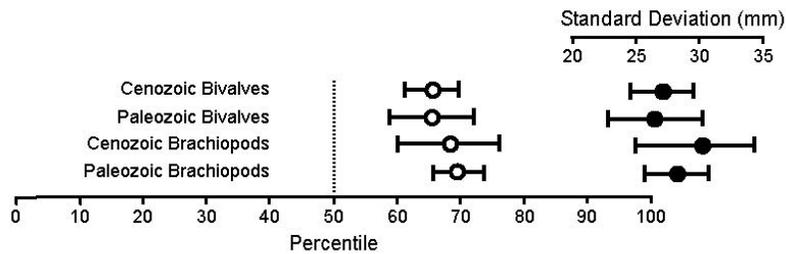


Figure 2.4 - Means (open circles) and standard deviations (filled circles) of percentile-frequency distributions. 95% confidence intervals were estimated by separate, 1000 iteration bootstrap simulations.

Species-Level Analysis

Figure 2.5 shows the results of the species-level analysis. In all cases, the scatter plots resemble the null model for biased yet predictable monographic measurements (Fig. 2.2B), because the slopes of the least-squares regression lines are close to unity, and the R-squared

TABLE 2.2 - Basic statistics for percentile distributions.

	N	Mean	Median	SD	Skew.	Kurt.
All Monograph Measurements	449	67.25	74.0	27.99	-0.72	-0.59
Bivalves	213	65.29	69.0	27.00	-0.60	-0.58
Brachiopods	236	69.01	80.0	28.79	-0.85	-0.52
Paleozoic Bivalves	60	65.12	70.3	26.57	-0.54	-0.72
Cenozoic/Recent Bivalves	153	65.36	68.5	27.25	-0.62	-0.51
Paleozoic Brachiopods	185	69.25	78.0	28.42	-0.85	-0.47
Cenozoic Brachiopods	51	68.16	81.5	30.38	-0.85	-0.66
Regional Distributions						
Bivalves: U.S./Caribbean	52	67.23	72.5	27.22	-0.77	-0.26
Bivalves: Europe	125	65.08	66.5	27.78	-0.55	-0.74
Bivalves: Other	36	63.22	65.8	24.31	-0.65	-0.07
Brachiopods: U.S.	205	68.27	78.5	29.48	-0.81	-0.60
Brachiopods: Other	31	73.95	83.0	23.57	-0.99	-0.33
Year-of-Publication Distributions						
Bivalves: 1960s-1970's	27	64.94	70.0	32.22	-0.56	-0.89
Bivalves: 1980's	121	65.04	66.5	27.66	-0.60	-0.60
Bivalves: 1990's	65	65.90	72.0	23.60	-0.59	-0.48
Brachiopods: 1960's	70	71.26	83.0	27.91	-1.03	-0.15
Brachiopods: 1970's	87	66.83	73.0	30.38	-0.71	-0.74
Brachiopods: 1980's	36	65.63	81.5	32.16	-0.77	-0.85
Brachiopods: 1990's-present	43	72.62	82.5	23.80	-0.82	-0.71
Monograph Sample Size						
Bivalves: n=1-25	64	63.01	66.25	28.47	-0.57	-0.63
Bivalves: n=26-50	45	60.38	64	25.42	-0.7	0.01
Bivalves: n=51-150	68	68.88	74.5	27.15	-0.67	-0.6
Bivalves: n=151-200	36	68.71	72.75	25.58	-0.56	-1.12
Brachiopods: n=1-25	41	74.72	82	24	-1.24	1.13
Brachiopods: n=26-50	77	65.75	78	32.37	-0.57	-1.15
Brachiopods: n=51-80	76	68.15	76.25	27.82	-0.79	-0.53
Brachiopods: n=81-250	42	71	81.25	27.82	-1.24	0.35

values are high and significant (Table 2.4). Logarithmic axes were used on each of the plots in Figure 6 as is appropriate for body size measurements. However, regressions were completed on both raw and log-transformed data, and showed similar results (Table 2.4). The intercepts of either regression can give an approximation of the amount of bias that is present in a particular group of the data. For example, monographed specimens of Paleozoic brachiopods are, on average, 1.63 mm larger than the average size of specimens from the bulk sample because the y-intercept of the least-squares regression line is 1.63 and its slope is nearly unity (Table 2.4).

Another way to visualize the amount of bias in a particular group is through the inset plots of residuals in Figure 2.5. Residuals were calculated from the line of equality, rather than from the least-squares regression line. Thus, a residual equal to zero in Figure 2.5 indicates a species with a monograph mean and bulk sample mean that are exactly equal to each other. The

residuals plots in Figure 2.5 show that for each group of the data, the majority of species had monograph means that were larger than their counterpart bulk-sample mean.

TABLE 2.3 - Percentile distribution comparisons for the primary data groups. Because of multiple pairwise comparisons, the Bonferroni correction must be applied. Thus, the significance criterion α must be $0.05/4 = 0.0125$.

	Wilcoxon Two-sample Test		Kolmogorov-Smirnov Two-sample Test	
	Z	p	D	p
Bivalves: Paleozoic<->Cenozoic	-0.116	0.908	0.08	0.945
Brachiopods: Paleozoic<->Cenozoic	-0.016	0.987	0.148	0.342
Paleozoic: Bivalves<->Brachiopods	-1.434	0.152	0.147	0.279
Cenozoic: Bivalves<->Brachiopods	0.923	0.356	0.229	0.036

Confounding Factors

Country of Publication: The country of publication of the monograph may be a factor that contributes to differences in the magnitude or consistency of monographic bias because authors from different countries may have different procedures for selecting specimens to photograph.

The percentile-frequency distributions constructed using regional grouping variables (Fig. 2.6) are similar to those shown earlier (Fig. 2.3) and are not significantly different from each other (Fig. 2.7; Table 2.5). However, the sample size for non-U.S. brachiopods may not be sufficient to make such a comparison. A similar result holds for species-level analysis of the regional data (Fig. 2.8). The two plots of Figure 2.8 have a strong resemblance to Figure 2.5 and to the null model for biased, but predictable monograph data (Fig. 2.2B). Again, residuals calculated from the line of equality show that the majority of monograph data in each group are biased toward larger sizes than their corresponding bulk sample mean size (Figure 2.8, inset plots). The statistical parameters for each least-squares regression show highly significant R-squared values with all slopes near unity (Table 2.4).

Year of Publication: With the advent of digital photography in the last ten years, one might expect that smaller shells can now be imaged in greater detail than in years past, thereby allowing authors to include images of smaller individuals in publications. Therefore, it is necessary to investigate the year of publication of each monograph as a possible confounding factor to the bias pattern illustrated above.

When year of publication is used as a grouping variable, percentile-frequency distributions for both bivalves and brachiopods (Fig. 2.9) bear a striking resemblance to the

TABLE 2.4 - Statistical parameters of regressions from species-level analysis. Regressions were performed on both raw and log-transformed data.

	Raw Data					Log-Transformed Data			
	N	slope	intercept	adj. r ²	p	slope	intercept	adj. r ²	p
Paleozoic Bivalves	16	1.07	1.81	0.87	<0.001	0.86	0.24	0.92	<0.001
Cenozoic/Recent Bivalves	28	1.09	0.87	0.96	<0.001	1.00	0.05	0.98	<0.001
Paleozoic Brachiopods	34	0.99	1.63	0.90	<0.001	0.92	0.14	0.92	<0.001
Cenozoic Brachiopods	10	1.07	1.00	0.96	<0.001	0.97	0.09	0.97	<0.001
Regional Distributions									
Bivalves: U.S./Caribbean	18	1.09	1.22	0.96	<0.001	1.00	0.05	0.99	<0.001
Bivalves: Europe	16	0.96	2.61	0.87	<0.001	0.92	0.16	0.80	<0.001
Bivalves: Other	10	1.08	1.13	0.88	<0.001	0.91	0.18	0.95	<0.001
Brachiopods: U.S.	33	1.00	1.90	0.91	<0.001	0.92	0.15	0.93	<0.001
Brachiopods: Other	11	1.10	-0.10	0.97	<0.001	0.98	0.06	0.97	<0.001
Year-of-Publication Distributions									
Bivalves: 1960s-1970's	14	1.02	4.01	0.92	<0.001	0.89	0.23	0.93	<0.001
Bivalves: 1980's	15	0.96	2.33	0.93	<0.001	0.92	0.15	0.88	<0.001
Bivalves: 1990's	15	1.23	-0.61	0.97	<0.001	1.01	0.05	0.98	<0.001
Brachiopods: 1960's	11	1.29	-0.25	0.85	<0.001	1.04	0.05	0.91	<0.001
Brachiopods: 1970's	11	0.72	5.25	0.64	0.002	0.71	0.38	0.73	0.001
Brachiopods: 1980's-2000s	22	1.07	0.37	0.95	<0.001	0.98	0.06	0.97	<0.001

pattern shown earlier in Figure 2.3. These distributions are also not significantly different from each other (Fig. 2.10; Table 2.5). The results of the species-level analysis on data grouped by year of publication are very similar to those detailed above as well (Fig. 2.11).

Sample Size: Finally, it is necessary to investigate the effect of the sample size that was available to the author at the time of publication. If an author is in possession of only a small number of specimens (≤ 10) of a species, then, in a sense, the exemplars of that species to be imaged in a publication have been pre-selected during collection. However, if a large sample of specimens is available, then an author must somehow choose a subset of those specimens to be imaged – potentially introducing another level of bias to these species.

Sample size groups for each clade are rather arbitrary and were chosen so that the data was divided as evenly as possible (Fig. 2.12). The histograms in Figure 2.12 clearly indicate the same type of monographic bias illustrated earlier. Again, these distributions are statistically indistinguishable (Tables 2.2, 2.5). Sample sizes for species-level analysis for data grouped by sample size were determined to be too small to yield meaningful regressions. Therefore, species-level comparisons, taking monograph sample size into account, were accomplished by plotting monograph sample size against a metric termed percent-difference (Fig. 2.13). Percent difference is derived from the mean sizes for the monograph and the bulk sample for each species. It is calculated by subtracting the bulk-sample mean size from the monograph-sample

mean size for each species. The resulting number is then divided by the bulk-sample mean size for that species and multiplied by 100. This metric is advantageous because it intuitively illustrates the difference in size between the bulk-sample mean and the monograph sample mean, expressed as a percentage of the bulk-sample mean. Figure 2.13 includes two plots, one each for bivalves and brachiopods. As expected, most species plot above the line of zero difference – this is the expression of the monographic bias. Both plots show rather wide scatter at small sample sizes and somewhat less scatter at large sample sizes. However, least squares regression lines through each dataset have slopes very close to unity (Fig. 2.13), which suggest that, on average, percent differences do not change appreciably as sample size increases. Thus, sample size seems to have no effect on the pattern of the monographic bias.

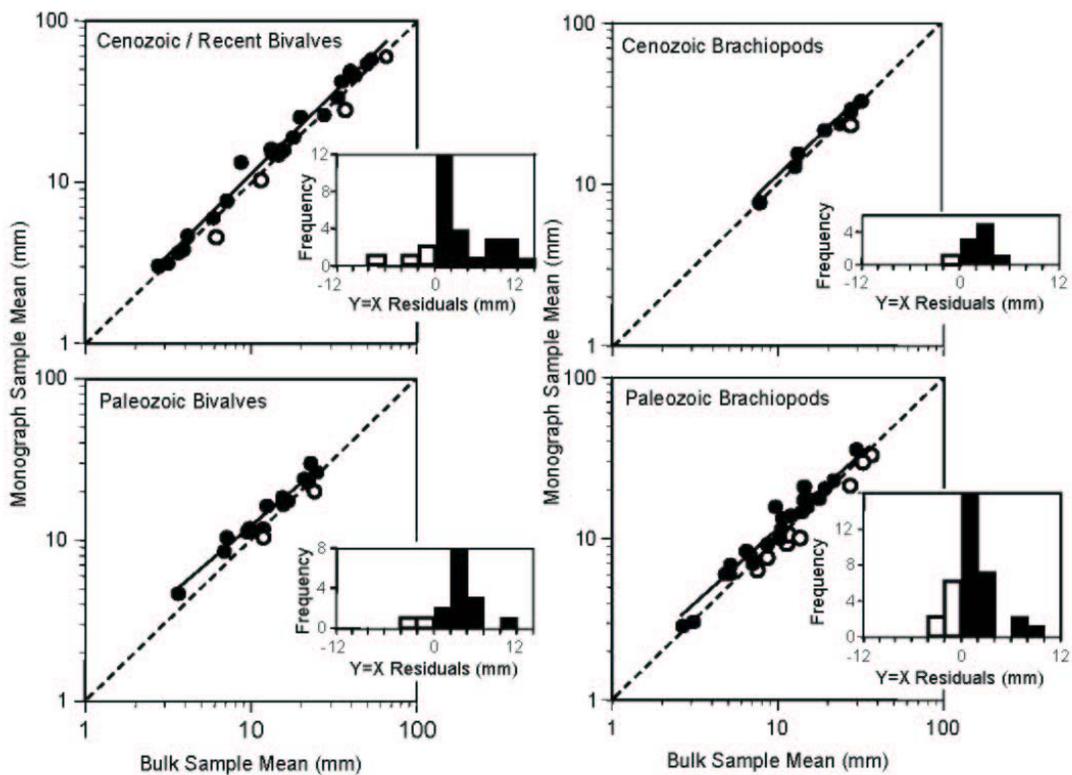


Figure 2.5 - Scatter plots with least-squares regressions showing the results of species-level analysis. Statistical parameters associated with these regressions are given in Table 2.4. Inset plots show residuals computed from the line of equality. Open symbols and white columns indicate monograph data that are biased in a negative direction with respect to the bulk sample.

TABLE 2.5 - Percentile distribution comparisons for data grouped by region, year of publication, and sample size.

	Kruskal-Wallis Test	χ^2	p
Bivalves: Regional Comparisons		0.83	0.66
Bivalves: Year-of-Publication Comparisons		0.16	0.92
Bivalves: Sample Size Comparisons		4.67	0.20
Brachiopods: Regional Comparisons		0.48	0.49
Brachiopods: Year-of-Publication Comparisons		1.08	0.78
Brachiopods: Sample Size Comparisons		1.19	0.76

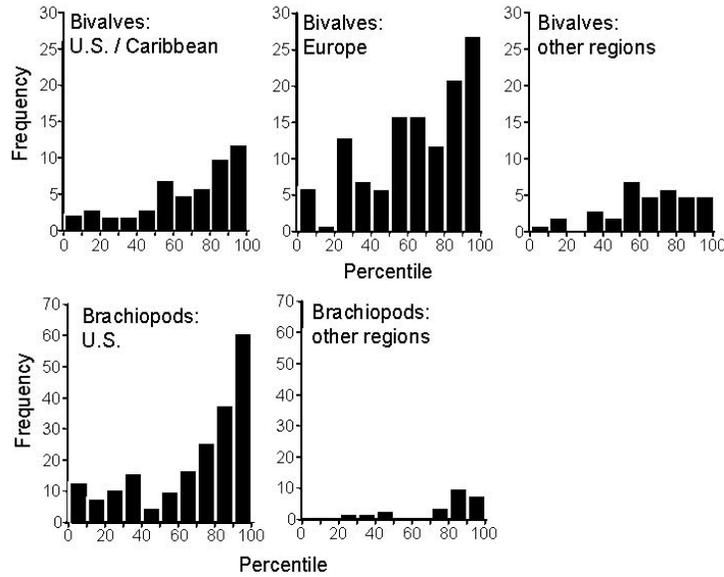


Figure 2.6 - Percentile-frequency distributions for bivalves and brachiopods, grouped by region from which monograph material was collected.

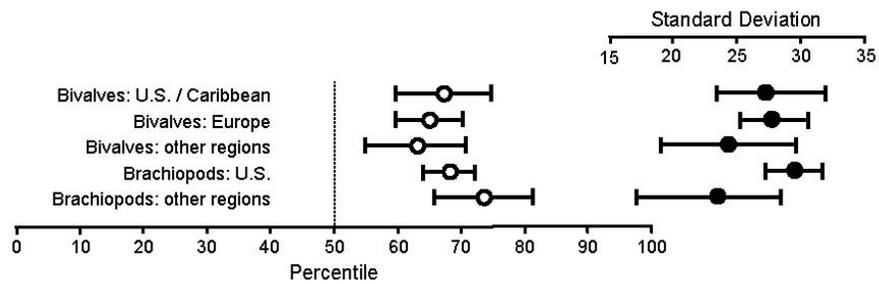


Figure 2.7 - Means (open circles) and standard deviations (filled circles) of percentile-frequency distributions grouped by geographical region. 95% confidence intervals were computed with separate, 1000 iteration bootstrap simulations.

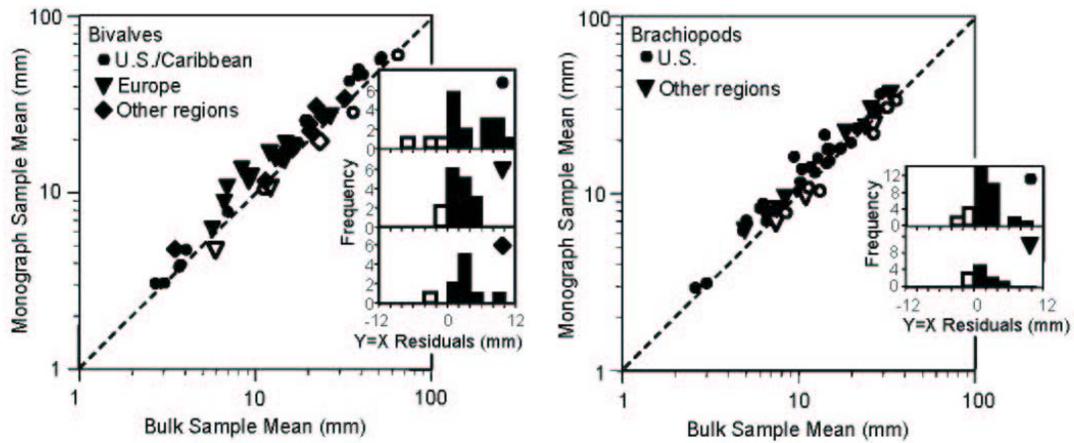


Figure 2.8 - Scatter plots with least-squares regressions showing the results of species-level analysis with data grouped by geographical region. Statistical parameters associated with these regressions are given in Table 2.4. Inset plots show residuals computed from the line of equality. Open symbols and white columns indicate monograph data that are biased in a negative direction with respect to the bulk sample.

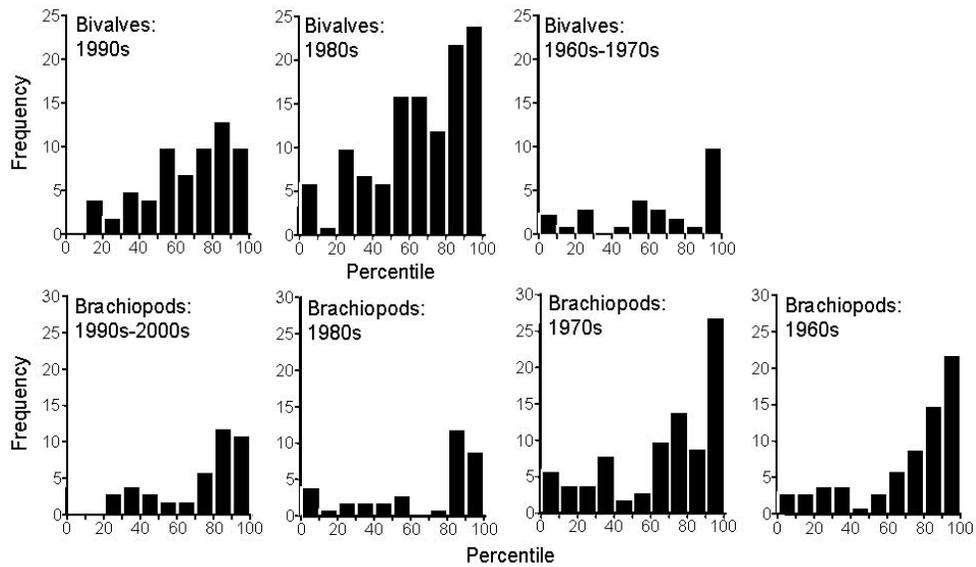


Figure 2.9 - Percentile-frequency distributions for bivalves and brachiopods, grouped by year of publication of the monographs from which data was collected.

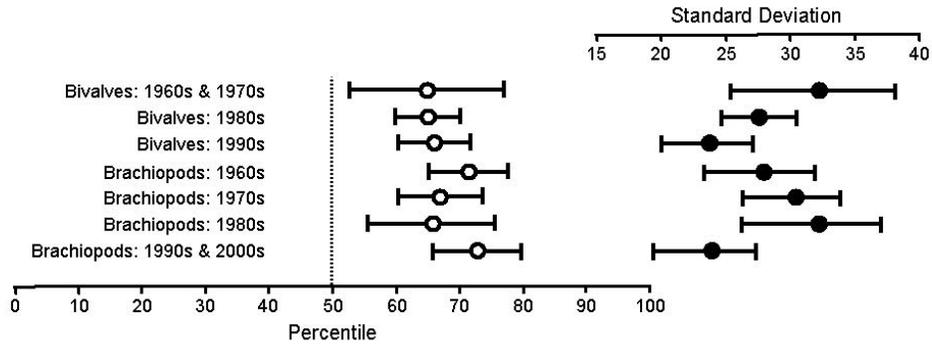


Figure 2.10 - Means (open circles) and standard deviations (filled circles) of percentile-frequency distributions grouped by year of monograph publication. 95% confidence intervals were computed with separate, 1000 iteration bootstrap simulations.

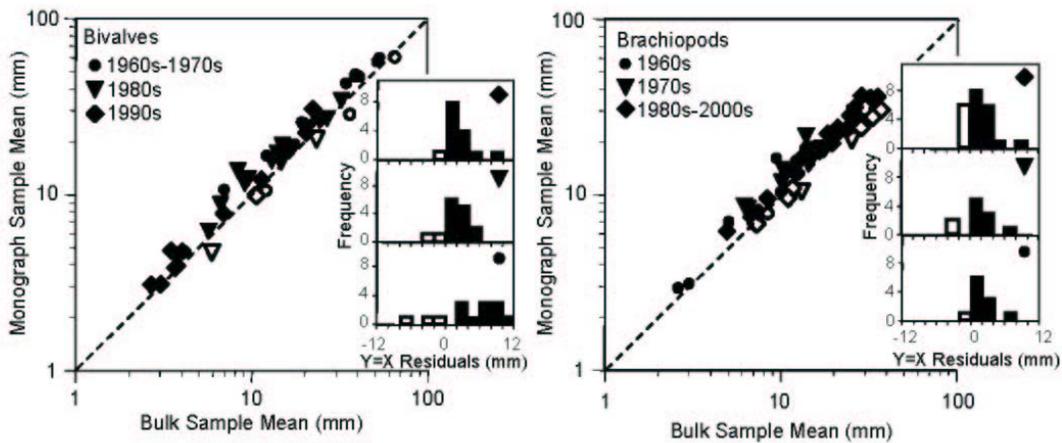


Figure 2.11 - Scatter plots with least-squares regressions showing the results of species-level analysis with data grouped by year of monograph publication. Statistical parameters associated with these regressions are given in Table 2.4. Inset plots show residuals computed from the line of equality. Open symbols and white columns indicate monograph data that are biased in a negative direction with respect to the bulk sample.

DISCUSSION

Characterization of the Bias

The principle goal of this paper has been to assess the quality of size measurements from images in monographs with respect to three parameters: bias direction, bias magnitude, and bias consistency.

Bias direction and magnitude can be ascertained from the specimen level analysis. The uniformity of the bias illustrated above is striking (Figs 2.3, 2.4). Authors of monographs seem to consistently choose a large size-class of specimens for illustration. Even though it may be an

inherent human trait to choose large things when presented with a size range (Gould, 1987), there may be another factor contributing to the bias.

The focus of most monographic studies is alpha-taxonomy. In order to adequately describe any species, one must first assemble a representative sample of specimens (Mayr et al., 1953; Blackwelder, 1967). From this sample, a suite of exemplars must then be chosen for photographic documentation. Intuitively, it is expected that the larger individuals in the sample would be chosen for this purpose because they often display a full suite of ontogenetic features that may be useful for species identification, and they may be easier to photograph as well. For these reasons it is not surprising to see a bias toward larger specimens in the monographic sample.

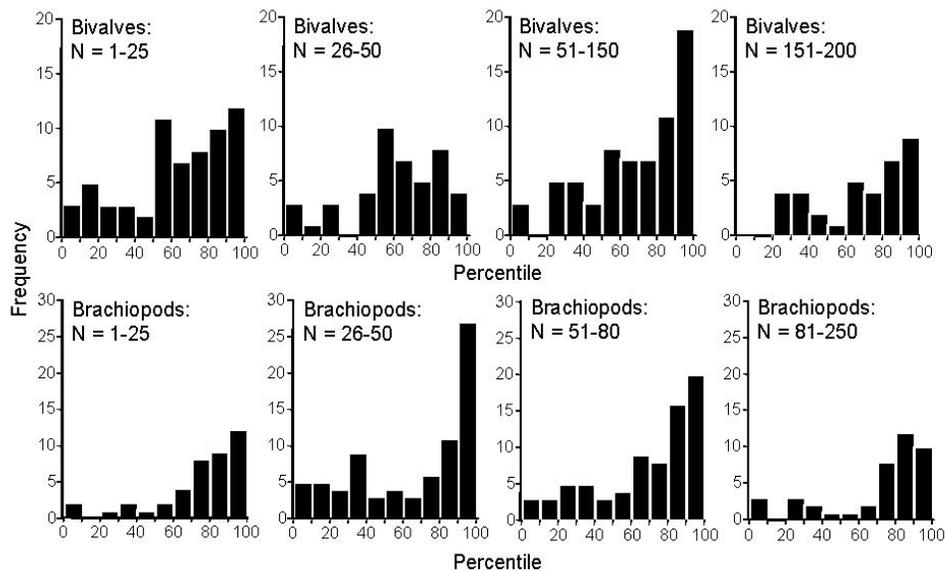


Figure 2.12 - Percentile-frequency histograms with data grouped by the sample size for the bulk sample of each species, as reported by the author of each monograph.

Yet, it also seems that authors do not simply choose to image the largest individual available. If they did, then the magnitude of the bias would be greater. Figure 2.4 indicates that the means of the percentile-frequency distributions for each data group are constrained to a narrow interval in the 65th to 69th percentile of the population size-frequency distribution (also see Table 2.2). Thus, the monographic data used here tended not only to be larger than the mean of the populations from which they were drawn; they also deviated from this mean by a very consistent magnitude.

Bias consistency can be further investigated using the species-level analysis. The results from the species-level analysis (Fig. 2.5) indicate a close resemblance to the scenario illustrated by Figure 2.2B. Each group exhibits a consistent, yet predictable bias toward larger monographic measurements. The bias can be considered consistent because the slope of the regression line for each group is close to unity (Fig. 2.5; Table 2.4), indicating that the magnitude of the bias does not change appreciably across a wide size range. The bias can be considered predictable because the adjusted R-squared values for each of the four main data groups are all high and significant.

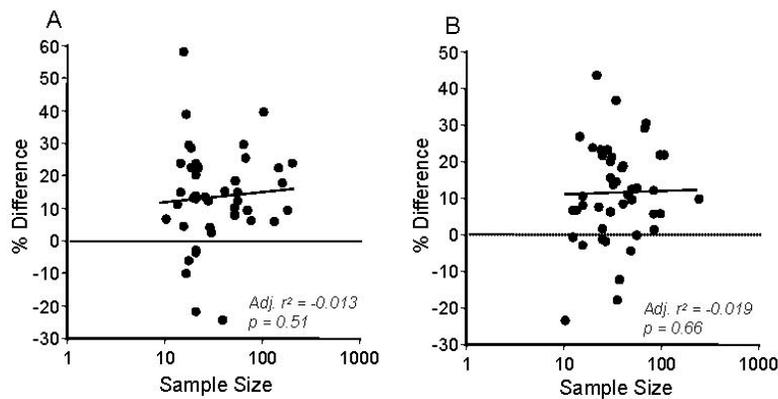


Figure 2.13 - Percent difference between monograph and bulk sample means for each species, plotted against sample size for the bulk sample of each species, as reported by the author of each monograph. See text for details on the calculation of differences. Dotted lines indicate no difference in mean size between the monograph and bulk sample for a species.

Taken together, these results point to a rather surprising outcome, monographic bias is highly consistent among different taxonomic groups. It is not entirely clear why this should be the case. It is possible that the unconscious tendencies of authors are exerting two opposing forces on these data. As mentioned above, authors may gravitate toward specimens somewhat larger than the mean of a population when choosing specimens to image, because these specimens are most likely to be adults displaying a full suite of ontogenetic characters. However, it is also possible that a tendency toward picking “representative” specimens, in terms of the size distribution of the population, may keep authors from only choosing the largest individuals to figure. The interplay between these tendencies may result in the bias illustrated here.

An Additional Confounding Factor

The results reported above indicate that the potential confounding factors of geography, year of publication, and sample size, have little effect on the overall pattern of monograph images yielding consistently larger sizes than bulk-collected specimens of the same species. However, an issue that has not been addressed is the fact that monograph sample sizes of less than ten were not included in these analyses so that bulk samples would be sufficiently large to construct a size-frequency distribution.

It is probable that many monographs feature species for which less than ten specimens are available. The analyses presented here cannot ascertain whether having very few specimens to photograph makes any difference to the monographic bias. Figure 2.13 suggests that as sample size decreases, the range of differences between species' monograph and bulk sample increase. Therefore, until the monographic bias for species with small sample size can be adequately studied, we advocate not using them in literature compilations of body size.

Implications

The highly consistent monographic bias reported here is good news for researchers interested in collecting meaningful size data from monographs. As long as one is aware of the presence and nature of bias, it can be taken into account and/or something can be done to correct for it. For this reason, this study does not advocate a change in the methodology of brachiopod and bivalve systematists. Furthermore, it can be shown that the monograph sample, though biased, provides a close approximation to the bulk sample in each case. Thus, relative changes in size through time ought to be detected equally well by both data types. An illustration of this point is given in Figure 2.14.

The monograph sample and the bulk sample for each species were compared by grouping bivalve and brachiopod data into epochs (Fig. 2.14). To construct this comparison, the mean size for each species was pooled with others from the same epoch. This was done separately for the monograph sample and the bulk sample. Once pooled by epoch, the mean of these means was calculated and 95% confidence intervals around this grand mean were computed with separate, 1000-iteration bootstrapping procedures.

These direct comparisons show how well the two datasets (monograph and bulk) track each other through time for both bivalves and brachiopods (Fig. 2.14). This suggests that even with a statistically significant bias toward larger specimens in monographs, mean values from the

two datasets are strikingly similar. Thus, size data compiled from either monographs or bulk samples would yield congruent trends through time for these groups.

It should be noted that Figure 2.14 is not intended to illustrate secular trends in body size for these groups; the data used to construct it are far too limited to address such an issue. Rather, Figure 2.14 merely illustrates the congruence between the monograph and the bulk sample for all of the species used in this study.

In summary, our results support the validity of the acquisition of size measurements from photographs in monographs. As a result, relative trends in monograph-derived body size measurements should be biologically meaningful.

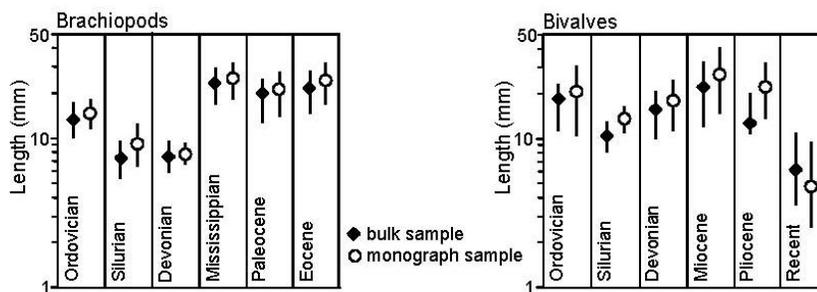


Figure 2.14 - Comparison of the mean of species means from the monograph and the bulk sample for each epoch in the dataset. 95% confidence intervals calculated with separate 1000 iteration bootstrap simulations. Sample sizes for each epoch are as follows: Brachiopods: Ordovician, 11 species; Silurian, 11 species; Devonian, 5 species; Mississippian, 7 species; Paleocene, 5 species; Eocene, 5 species. Bivalves: Ordovician, 3 species; Silurian, 7 species; Devonian, 6 species; Miocene, 9 species; Pliocene, 16 species; Recent, 3 species.

CONCLUSIONS

Size measurements of images of specimens in the taxonomic literature can be used to study body size history. Such measurements represent a biased sample with respect to the mean size of the population from which they were drawn, but the bias is similar among unrelated species.

Most specimens studied came from the 65th to 69th percentile of their species' bulk-collected size-frequency distribution. This indicates a significant bias toward monograph specimens that are larger than the mean size of the bulk sample. When compared at the species level, this bias was found to be highly consistent among the 86 species included in the study. Thus, size measurements of monographed specimens of bivalves and brachiopods reliably and consistently record a similar size class for any given species. This is true regardless of taxonomic affinity, collection locality, and age of the specimens.

The consistency of these results suggests a worker-induced bias that may occur because of tendencies to choose larger, but not the largest, specimens as exemplars of a species. If this is the case, then studies of this type on other groups may yield similar results. However, we do not advocate a change in taxonomic methodologies. The consistency and predictability of the bias makes it easy to correct for during meta-analyses.

Even when left uncorrected, monograph derived size data closely approximate size trends exhibited by measurements on bulk-collected specimens. This enables the paleontologist to utilize two complementary sources of data, so long as they are not mixed in the same analysis. Field-collected specimens and images in monographs can be used as parallel, independent data sources in the study of macroevolutionary size trends among major clades. Thus, images of specimens in monographs represent vast archives of paleoecological information that can, and should, be used to advance our knowledge of the history of life.

CHAPTER THREE¹: Comparative time averaging: Age mixing among sympatric bivalves and brachiopods from a modern tropical shelf

¹ This chapter will be submitted for publication to the journal *Paleobiology* in May 2006. The co-authors for this publication, Susan L. Barbour Wood, Michał Kowalewski, John F. Wehmiller and Marcello G. Simões, contributed less than 20% to the data collection and analysis stages of this project. The text was written completely by R.A. Krause.

Abstract

Relatively little is known of how time averaging of marine skeletal accumulations compares among different species in a single locality. Here we provide quantitative data on the time averaging magnitude of two species with divergent physical and ecological characteristics, the terebratellidine brachiopod *Bouchardia rosea* and the tellinacean bivalve *Semele casali*, collected from two sites (10 m and 30 m depth) off the coast of Brazil in Ubatuba Bay (Southeast Brazilian Bight, SW Atlantic). These two species co-occur in large numbers throughout this tropical mixed carbonate-siliciclastic shelf, and this setting provides a good climatic and environmental analog to brachiopod- and bivalve-rich shell beds in Paleozoic successions of North America and Europe.

A total of 161 individual shells were dated using amino acid racemization (D/L aspartic acid) calibrated with eighteen AMS radiocarbon dates. The dated shells ranged in age from modern to 12,000 years with a semi-quartile range of 1300 years for brachiopods and 1400 years for bivalves. The age distributions for each grouping of the data were strongly right-skewed and dominated by shells less than 3000 years old. The data grouped by species and by site indicates some significant differences in time averaging magnitude (as measured by the semi-quartile range). Comparison of brachiopods at the two sites indicates that specimens taken from the 30 m site are significantly more time averaged than specimens from the 10 m site. No significant difference is seen in bivalves from the two sites. The most time averaged species from the 10 m site is *S. casali*, whereas the most time averaged species from the 30 m site is *B. rosea*. These differences among sites are attributed to stochastic variation in the intensity of taphonomic processes and frequency of exposure at the sediment-water interface. When the data for each species are pooled, bivalves and brachiopods show very similar time averaging magnitude. Analysis of the completeness of each sample, using a Monte Carlo model that simulates 100% complete uniform or exponential distributions, indicates that brachiopods and bivalves were both likely drawn from 100% complete exponential distributions, although individual sites exhibit appreciable variation in their putative underlying distributions.

These findings imply an independence of the intrinsic physical characteristics of an organism and time averaging magnitude, at least among commonly fossilized organisms. Furthermore, our findings suggest that time averaging magnitude and water depth may be rather closely related. A meta-analysis of previously published shell ages confirms this pattern for

several different latitudes and environments indicating that time averaging magnitude and depth may have a very similar positive correlation regardless of the depositional system.

Introduction

The temporal resolution of the fossil record is an important determinant of the types of biological and environmental information that can be discerned from the geologic past. It is well known that most fossiliferous deposits are subject to a suite of postmortem processes that lead to varying degrees of temporal mixing or time averaging. Since this phenomenon results from the interaction of many quasi-independent factors, such as physical reworking, transport, and bioturbation (Martin 1999), the extent of time averaging can be quite variable among different environments (Kidwell and Bosence 1991; Walker and Voight 1994) and taxa (Kowalewski 1996a, 1997).

The magnitude of time averaging of a fossiliferous deposit is not easily estimated from the fossil record because dating techniques typically do not provide sufficient resolution, especially in deposits older than several million years (Brett and Baird 1993; Kidwell 1993). This problem can be circumvented by using indirect methods such as stratigraphic bracketing with scattered radiometric dates (Kidwell and Bosence 1991), or by dating shells from modern sediments and using them as an analog for ancient deposits. The latter method has been used with increasing frequency in the last decade (Flessa et al. 1993; Wehmiller et al. 1995; Goodfriend and Stanley 1996; Martin et al. 1996; Anderson et al. 1997; Meldahl et al. 1997; Flessa 1998; Kowalewski et al. 1998; Carroll et al. 2003; Kidwell et al. 2005), and has yielded average age ranges of 10^2 - 10^4 yr for marine molluscan assemblages.

Despite this body of work, little is known of time averaging in organisms other than mollusks (Behrensmeier et al. 2000; but see Carroll et al. 2003). As a result, it is difficult to determine how time averaging may vary among sympatric organisms (Martin et al. 1996). Furthermore, the overprint of different life modes, skeletal mineralogy, and intrinsic durability on the time averaging signature of organisms is poorly understood. Here we present quantitative data on comparative time averaging for two sympatric bivalves and brachiopods. We focus on these organisms because they are common components of the marine biota through much of the Phanerozoic and one or the other of these taxa have been important contributors to shell beds since the Ordovician (Kidwell and Brenchley 1996). These two taxa differ markedly in their mode of life, as well as their skeletal mineralogy. Yet they are often found in similar environments throughout their stratigraphic ranges. This makes them good candidates for a comparative study of time averaging.

Material for this study was collected from Ubatuba Bay of the Southeast Brazilian Bight marine province. This area is one of the few places in the world where brachiopods and bivalves co-occur in appreciable numbers in a sub-tropical, open-shelf setting (Kowalewski et al. 2002; Simões et al. 2004). As such, this locality provides a unique opportunity to assess the time averaging characteristics of incipient bivalve and brachiopod shell beds accumulating in an environment that is closely comparable to Paleozoic shelves.

Background

Study Area

Ubatuba Bay, a small embayment located off the coast of the state of São Paulo, Brazil, is a part of the Southeast Brazilian Bight Marine Province (Campos et al., 1995; Mahiques et al., 2004). The area is situated at 23° south latitude and is characterized by a humid tropical climate. Water depths throughout the bay are shallow (0-30 m in the sampled area), salinity is fully marine (34-35‰), and the mean annual temperature is ~24° C. Oceanographic studies (Campos et al. 1995, 2000) indicate that the region is dominated by water masses of the South Brazil Current, a warm west-boundary current flowing from the equator. The area also experiences seasonal shelf-break upwelling associated with cyclonic meanders of the South Brazil Current, which bring cold (<20°C) nutrient-rich waters of the South Atlantic Central Water up onto the inner shelf (Campos et al. 1995, 2000; Braga and Muller 1998). The two sites investigated in this study are also regularly influenced by the Coastal Water mass and can intermittently experience fresh-water plumes associated with increased coastal runoff (Campos et al. 1995, 2000).

The sediments of the inner shelf are mixed, but dominated by terrigenous clastics (~75wt%, Table 3.1). The median grain sizes of these sediments are highly variable, but the collection sites for this study were dominated by coarse sands and some gravel (Table 3.1). Shell material, dominated by brachiopods, mollusks, echinoids, bryozoans, and foraminifers, is also locally abundant and becomes more common toward the outer portions of the bay (Mahiques 1995; Mahiques et al. 1998; Mantelatto and Fransozo 1999; Kowalewski et al. 2002; Simoes et al. 2004; Barbour Wood et al. *in review*). Brachiopods and bivalve mollusks are particularly abundant wherever shell material is present, and two of the most common constituents of the fauna are the terebratellid brachiopod *Bouchardia rosea*, and the tellinacean bivalve *Semele casali*.

Bouchardia rosea

The brachiopod used in this study, *Bouchardia rosea* (Mawe), has a fossil record going back to the Cretaceous (Mañcenido and Griffin 1988), but is restricted to the Southern Hemisphere. It is a sessile epifaunal benthic organism that is free lying (Richardson 1981; Brunton 1996) and inhabits substrates with carbonate concentrations ranging from 40-70%

Table 3.1: Sediment characteristics for the two collection sites.

Site	Ubatuba 1	Ubatuba 9
Depth (meters)	30 m	10 m
Latitude	23° 28' 53" S	23° 26' 41" S
Longitude	44° 55' 21" W	45° 02' 07" W
Temperature (°C)	21.2	21.4
Salinity (‰)	35	34
Gravel (%)	6.69	24.12
Very coarse sand (%)	7.61	14.43
Coarse sand (%)	56.63	29.81
Medium sand (%)	20.64	18.04
Fine sand (%)	4.55	4.81
Very fine sand (%)	0.61	1.83
Mud (%)	3.28	6.97
Mean diameter (phi)	0.55	0.13
Mean diameter (mm)	0.68	0.91
Standard deviation	0.91	1.3
Skewness	-0.27	0.16
Kurtosis	4.15	2.34
Sorting (Folk, 1974)	moderate	poor
Percent carbonate	25	25
Percent organics	3	7

(Simoes et al. 2004; Kowalewski et al. 2002). Specimens are generally small (<20 mm), but robust, and are characterized by a low Mg calcite shell that has a punctate fabric. The species is further characterized by a brachidium with a simple calcareous loop and a strong hinge structure (Brunton 1996). Like other brachiopods of this order (Terebratulida), the shell of *B. rosea* is composed of a thin primary shell layer, a thick, fibrous, secondary shell layer, and lacks a tertiary layer (Rudwick 1970). The fibrous shell layer is characteristic of extant terebratulides and rhynchonellides. This feature was also common in Paleozoic members of these groups (Williams et al. 1997), and was the standard fabric for all spire-bearing brachiopods, pentamerides, and most orthides (Williams and Rowell, 1965). Thus, the shell structure of *B. rosea* is very similar to the type that has been dominant among Rhynchonelliformea throughout the Phanerozoic, except perhaps during the Permo-Carboniferous (Williams et al. 1997)

Semele casali

The bivalve used in this study, *Semele casali*, is an infaunal, facultative deposit feeder that burrows in silt, sand, or mud to a depth of 5 cm, although larger specimens have been

recovered from a depth of 11 cm (Narchi and Domaneschi 1977; Domaneschi 1995; Stead et al. 2002). The aragonitic shell is generally small (<20 mm), and thin with weak concentric sculpture present on the entire external surface of both valves (Narchi and Domaneschi 1977). Specimens of *S. casali* have been recovered from the southwestern Atlantic from 20-35° S, and a depth range of 10-180 m (Narchi and Domaneschi 1977).

The tellinacean genus *Semele* has a wide distribution in the tropical and temperate oceans of the northern and southern hemisphere. It is particularly abundant in the eastern Pacific, where 28 species are currently recognized (Coan 1988). The western Atlantic has far fewer extant species, (only six, including *S. casali*), but there were far more species in this area in the Tertiary (Boss 1972; Domaneschi 1995). The Semelidae evolved rather recently, in the Eocene, but the superfamily Tellinacea has a fossil record going back to the late Triassic. The earliest representatives were probably very shallow infaunal suspension feeders judging from their lack of a pallial sinus, but the deeper burrowing habit seen in *Semele casali* had evolved by the late Jurassic (Pohlo 1982). Thus, this species represents a shell type and life habit that has been common throughout most of the Mesozoic and Cenozoic.

Dating Technique

To estimate the scale of time averaging among these two species, we employ here amino acid racemization (AAR) calibrated with accelerator mass spectrometry (AMS) ¹⁴C dating. This method has been used with increasing frequency in the last several decades because it has proven reliable and efficient for dating large numbers of specimens (Wehmiller 1982; Miller and Hare 1980; Hearty 1987; Miller et al. 1987; Goodfriend 1987, 1991). It has been applied to a wide variety of biomineralized fossils and subfossils, including marine organisms (forams, corals, mollusks, and brachiopods), terrestrial organisms (egg shells, mollusks, plants, bones, teeth), and other biogenic materials (Goodfriend 1989; Wehmiller et al. 1995; Goodfriend et al. 1996; Blackwell et al. 2000; Kaufman, 2000; Keil et al. 2000; Kimber and Griffin 2000; Manley et al. 2000; Teece et al. 2000; Waite 2000). In particular, several studies focused on time averaging rates among marine mollusks and, to a lesser extent, brachiopods have successfully employed this technique in multiple Holocene, and in some cases Pleistocene environments (Powell and Davies 1990; Flessa et al. 1993; Flessa and Kowalewski 1994; Wehmiller et al. 1995; Martin et al. 1996; Meldahl et al. 1997; Kowalewski et al. 1998, 2000; Carroll et al. 2003).

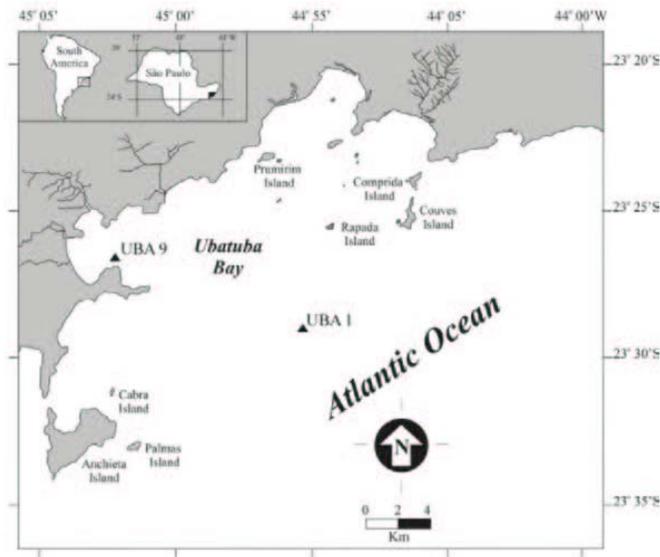


Figure 3.1 - Study area and collection sites. UBA 1 = 30 m site; UBA 9 = 10 m site. Modified from Barbour Wood et al. *in review*.

Materials and Methods

Sample Collection

Samples were collected as a part of an ongoing project of the marine ecology group of the São Paulo State University. The collection sites for this study were both on the inner shelf in Ubatuba Bay (Fig. 3.1). One site was at a depth of 30m meters and was dominated by coarse and medium grained sands. The other site was in 10m of water and was dominated by coarse sands and gravel. Samples were collected using a Van Veen grab sampler ($1/40 \text{ m}^2$), which collects material from the uppermost several centimeters of the substrate. Brachiopod and bivalve material were separated, counted and identified to species level for each sample. From each site, a suite of specimens of the aragonitic bivalve *Semele casali* (10m: n=36; 30m: n=36), and the calcitic brachiopod *Bouchardia rosea* (10m: n=30; 30m: n=28), were chosen randomly from among all collected specimens for amino acid dating.

Amino Acid Racemization Dating

The age estimate for each shell was obtained by analysis of the amino acid racemization (AAR) of a single shell fragment. In each case, the shell fragment was taken from the same location on the shell to minimize intra-shell variability in racemization rate (Goodfriend et al.,

1997; Carroll et al., 2003). For brachiopods we sampled the secondary, fibrous shell layer on the outer margin of each shell directly opposite the hinge, for bivalves, sampling was done near the outer margin of the shell halfway between the anterior and posterior side. These shell fragments were then processed according to the procedure outlined by Carroll et al. (2003) and Barbour Wood et al. (in review), and analyzed for the D and L enantiomers of aspartic acid.

In addition to 129 new shells, we also include here 32 brachiopod shells that were amino acid dated in an earlier study (Carroll et al. 2003), and were collected from the same 10 m site that we use in this study. These shells were originally dated using alloisoleucine / isoleucine (A/I) ratios, but they were reanalyzed for aspartic acid. We found a high positive correlation between A/I and Asp values for these shells, suggesting that both of these amino acids can be utilized for dating both mollusks and brachiopods (Barbour Wood et al. *in review*).

From the 161 shells subjected to AAR analysis, a sub-sample of 18 shells was chosen for radiocarbon analysis at the NOSAMS Laboratory at Woods Hole Oceanographic Institute. This sub-sample was chosen non-randomly to maximize the range of D/L Aspartic (Asp) values for each taxon and site. The absolute ages for this sub-sample of shells were determined using CALIB (v. 5, Stuiver et al., 2005). The Asp values of the calibrated shells were then used to determine the ages of the remainder of the sample using the equations below, which are derived from least-squares regression lines through each data group.

$$(1) \quad Age_{10m}^{Bouchardia} = \left(Asp^{2.6} - 0.0127 \right) / 4.63 \times 10^{-05}$$

$$(2) \quad Age_{30m}^{Bouchardia} = \left(Asp^{2.6} - 0.0104 \right) / 3.82 \times 10^{-05}$$

$$(3) \quad Age_{10m}^{Semele} = \left(Asp^{3.1} - 1.35 \times 10^{-04} \right) / 1.14 \times 10^{-05}$$

$$(4) \quad Age_{30m}^{Semele} = \left(Asp^{3.1} - 6.55 \times 10^{-04} \right) / 6.44 \times 10^{-06}$$

The aspartic acid ratio and calculated age for each shell is given in Appendix 3.1. For a thorough discussion of the calibration of the radiocarbon dates and the derivation of equations 1-4 refer to Barbour Wood et al. (*in review*).

Ages calculated using equations 1-4 are subject to the errors involved with the analytical techniques. The measurement error for aspartic acid can be calculated as the average range in values for the 2-5 replicates analyzed from each shell fragment. The average range of Asp values from a single shell in this study is 0.02, which amounts to a measurement error of ~7%

using an average Asp value of 0.3. Because this error behaves in a percent-wise rather than an amount-wise manner, its effects increase with age (Wehmiller and Miller 2000), and when propagated through the age equations this error can cause age fluctuations in a single shell of more than 100 years. Thus, to minimize this error, the Asp values used to calculate ages in this study are the average of all the replicates for each shell. Uncertainties in uncalibrated and calibrated radiocarbon years were much less than those for amino acid racemization. The uncertainties for uncalibrated radiocarbon ages (as reported by NOSAMS) ranged from 25 to 90 years and averaged 35 years, while the uncertainties involved with the calibration averaged to 94 years (Barbour Wood et al. *in review*). Finally, for both species, the range of radiocarbon dates is less than the total range of the sample. As a result, shell ages calculated to be older than these radiocarbon-dated shells have a significant amount of uncertainty associated with them. However, the portion of the dataset affected by this uncertainty is rather small; most of the calculated shell ages are considered very reliable. Specifically, we are most confident about the ages for bivalves that are younger than 3000 years (76% of dated bivalves), and brachiopods that are younger than 7000 years (96% of dated brachiopods).

Quantification and Comparison of Time Averaging

Quantification of time averaging can be accomplished using several different dispersion metrics. Many previous workers have used the range in ages for a site as an estimate of the magnitude of time averaging (Flessa et al. 1993; Flessa and Kowalewski 1994; Meldahl et al. 1997). However, range is based on extreme outliers, and is thus particularly sensitive to sample size. Other studies have used the shell half-life to quantify time averaging (Cummins et al. 1986; Meldahl et al. 1997). This technique estimates the amount of time needed to remove 50% of the shells that were initially present, using a best-fit exponential curve for the age-frequency distribution. The problem is that this method assumes a constant input of shells through the entire interval and is sensitive to the binning that is used. Other metrics that are commonly used are the standard deviation (Kowalewski et al. 1998) and the semiquartile range of the age-frequency distribution for a site (Kidwell et al. 2005).

Here we focus on the semi-quartile range (SQR), but report several other metrics for comparison with previous studies (Table 3.2). SQR is calculated as the difference between the first and third quartile (25th and 75th percentile), divided by two. In other words, SQR is one-half of the inter-quartile range. It is an intuitive metric because it is reported in the original

Table 3.2: Descriptive statistics for all age-frequency distributions.

	Brachiopopds		Bivalves		Brach.	Bivalves	All
	30m	10m	30m	10m			
Sample Size	28	62	36	35	90	71	161
Dispersion Metrics							
Range (years)	8675	4596	12342	11908	8675	12342	12342
Standard Deviation (years)	2757	1216	2857	3340	2317	3103	2686
Confidence Intervals around SD							
99% lower bound (years)	2128	867	1109	1838	1653	1870	2082
95% lower bound (years)	2311	942	1431	2283	1895	2220	2213
95% upper bound (years)	3168	1457	4080	4243	2698	3863	3160
99% upper bound (years)	3274	1522	4414	4428	2783	4062	3316
Confidence Intervals around SQR							
99% lower bound (years)	1556	419	374	818	812	528	922
95% lower bound (years)	1820	522	452	1158	950	729	1056
95% upper bound (years)	3166	1338	1825	3389	1973	1954	1815
99% upper bound (years)	3354	1383	2355	4708	2088	2185	1918
Other descriptive statistics							
Median shell age (years)	4089	438	750	700	922	708	869
Mean shell age (years)	4048	974	1801	2520	1930	2155	2029
Minimum shell age (years)	0	0	0	12	0	0	0
Maximum shell age (years)	8675	4596	12342	11920	8675	12342	12342
Quartile 1	1107	0	123	105	189	107	151
Quartile 3	6508	1906	2006	3888	2808	2925	2808
Semi-quartile range	2700.5	953	941.5	1891.5	1309.5	1409	1328.5
Skewness	0.06	1.33	2.57	1.53	1.32	1.93	1.78
Kurtosis	-1.47	0.9	6.73	1.48	0.74	3.06	2.88

measurement units (years in this case), and it eliminates some of the problems associated with other measures of dispersion, such as the assumption of continuous shell input and the sensitivity to binning and sample size. Furthermore, unlike the standard deviation, SQR is appropriate for highly skewed distributions because it is not affected by outliers (Sheskin 2004).

To facilitate comparisons among the SQR values for each site and taxon, confidence intervals around these values were calculated using a balanced bootstrap (Hall 1992; Kowalewski 1996b; SAS/IML code for confidence intervals around SQR is given in Appendix 3.2). Bootstrapping is useful in this case because it avoids the assumptions of parametric tests (normally distributed data) and commonly has more power than non-parametric tests (Diaconis and Efron 1983; Manly 1991). Each sample was resampled with replacement for a pre-determined number of iterations. Pilot bootstrap analyses indicated that estimates of SQR

stabilized after approximately 4000 iterations. Thus, we report here confidence intervals constructed from 4999 iterations for SQR. In addition, to the random samples, we included in each case the SQR for the original sample to make 5000 total bootstrap iterations (Manly 1991). SQR was calculated for each of the bootstrapped samples and the 0.5, 2.5, 97.5, and 99.5 percentiles of the resulting sampling distribution were used to estimate the 95% and 99% confidence intervals (Efron 1981). For each sample, the bootstrap estimates showed a bias toward smaller values than the actual SQR. This is a common problem when bootstrapping dispersion metrics because random samples will often have less variation than the original sample, but rarely will they have more. To correct for this bias, the mean SQR from each bootstrap distribution was standardized to value for the original sample (see Kowalewski et al. 1998). The magnitude of this bias was rather variable among the samples (10-200 years) but it did not affect our interpretations. Thus, more intensive correction methods such as accelerated bias correction (DiCiccio and Romano 1988) were deemed unnecessary.

Completeness Analysis

The age-frequency distributions obtained in this study can offer insight into the temporal completeness of the fossil record encompassed by the time averaged samples. This is analogous to paleontological or stratigraphic completeness (Sadler 1981; Allmon 1989), and can be defined as the percent of the time intervals, within the time span of a sample, that are represented by a paleontological record (Kowalewski et al. 1998). The resolution used in this study is 100 years, because this is the highest resolution that can be considered given the accuracy and precision of amino acid dating and the size and age range of our samples. It is important to note that since completeness is a scale dependent phenomenon (Sadler 1981); any distribution can appear complete or incomplete depending on the scale of observation. For example, because of the chosen resolution for this study, and the size of the samples, it is impossible to obtain a 100% complete record for three of the four samples considered here (i.e. there are more bins than specimens). The maximum possible completeness for a sample can be calculated as the sample size divided by the number of time bins, where the number of time bins is the range of the sample divided by the resolution (Table 3.3). From these values it is apparent that gaps due to sampling are inevitable, but it is possible to determine how complete we could expect a sample to appear, given its size, range, and an assumption of its underlying distribution.

Table 3.3: Results of completeness simulations. See text for descriptions of uniform and exponential distributions.

	Brachiopods		Bivalves		Brach.	Biv.	All
	30m	10m	30m	10m			
Sample Size	28	62	36	35	90	71	161
Maximum possible completeness (%)	32.2	100	29	29.2	100	57.2	100
Completeness analysis (100-year resolution)							
Observed completeness (%)	27.6	52.2	18.5	16.7	43.7	29	45.2
Uniform distribution (100% complete)							
Expected completeness (%)	27.8	74.5	25.4	25.6	64.9	43.8	73.1
Confidence intervals around expected							
99% lower bound (years)	23.1	63.1	63.1	21	56.5	37.3	65.6
95% lower bound (years)	24.2	65.3	65.3	22.7	57.6	38.9	68.1
95% upper bound (years)	31.1	82.7	82.7	28.6	71.5	47.8	78.6
99% upper bound (years)	32.3	87	87	28.6	73.8	49.4	80.2
Probability of 100% completeness	0.33	0.001	0.001	0.001	0.001	0.001	0.001
Exponential (right-skewed) distribution (100% complete)							
Expected completeness (%)	23.2	49.7	21.2	21.5	44.4	32.9	48.6
Confidence intervals around expected							
99% lower bound (years)	17.3	37	17	16.8	35.7	25.9	41.3
95% lower bound (years)	18.4	39.2	17.8	18.5	38	28.4	42.9
95% upper bound (years)	27.7	58.7	24.3	25.2	50.7	38.1	54.3
99% upper bound (years)	30	60.9	25.1	26	53	38.9	55.9
Probability of 100% completeness	0.037	0.366	0.052	0.003	0.37	0.043	0.116

With respect to the underlying age-frequency distributions of the samples in this study, there are two possibilities that will be assessed. First, we will test for what can be conceived as the best-case scenario for the fossil record, that is, a 100% complete record with uniform and continuous input of new material in each time interval, and no taphonomic loss of old shells. Second, we will test for a scenario in which the fossil record is 100% complete, but the chance of obtaining a paleontological record for a given interval decreases exponentially for each time step. This is a more realistic scenario because the longer skeletal material is around; the more likely it is to be removed from the sediment-water interface by burial or the processes of taphonomic destruction (Kidwell and Bosence 1991; Olszewski 1999, 2004).

We performed seven independent Monte Carlo simulations (one for each sample; one each for pooled brachiopods and bivalves; one for all of the data) in which we randomly sampled from 100% complete uniform and exponential distributions (SAS code for these simulations are in Appendix Three; also see Kowalewski et al. 1998). For each of the four samples, with sample size k and observed age-range r , we drew k observations from each simulated distribution with a

range of r . For each simulation, 999 random samples were generated and their completeness was calculated at a resolution of 100 years. Again, the addition of the observed completeness value for each sample yields a sampling distribution of 1000 completeness estimates (Manly 1991), from which confidence intervals can be calculated from the 0.5, 2.5, 97.5, and 99.5 percentiles.

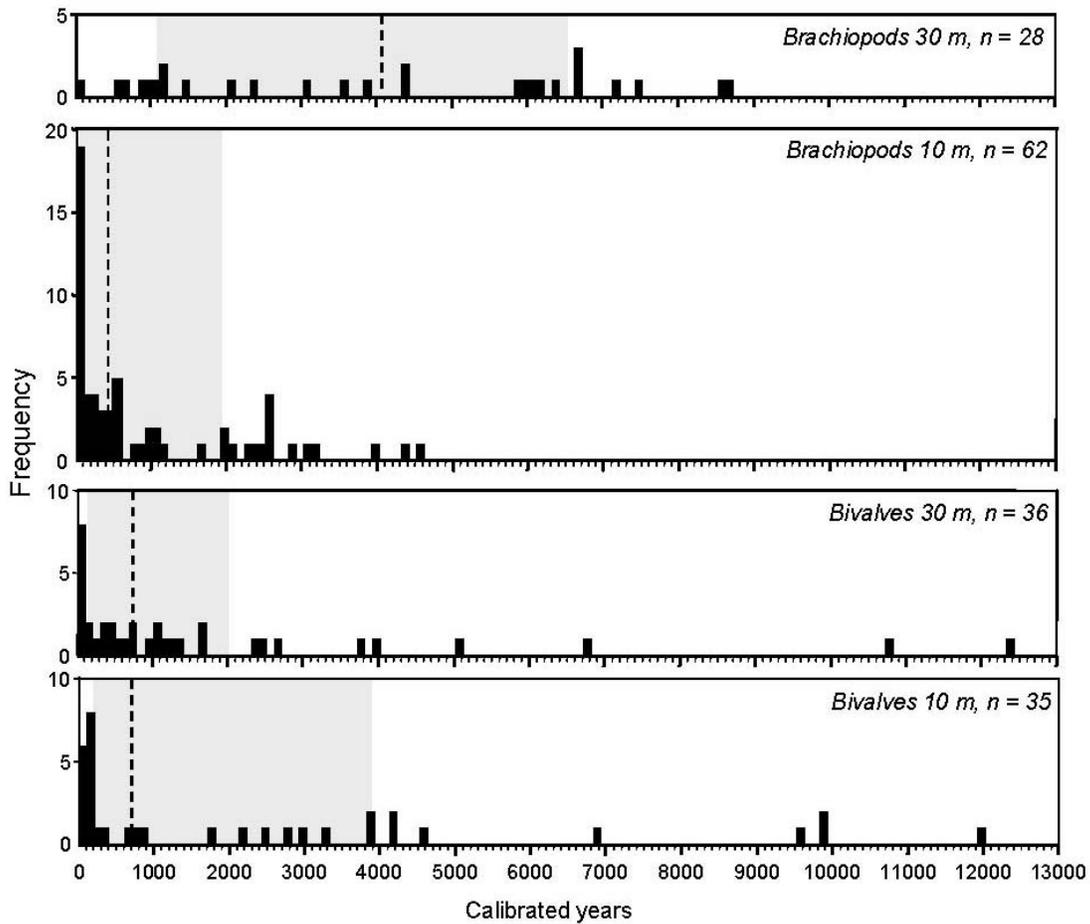


Figure 3.2 - Age-frequency distributions for each species and site. Ages were calculated using D/L aspartic acid values calibrated with several radiocarbon dates. The shaded area behind each distribution delineates the inter-quartile range and the dotted lines indicate the median age for each distribution.

Results

Magnitude and Variation of Time Averaging

The 161 shells dated in this study range in age from 0 (not live collected) to 12342 years, although 76% of the shells are from the last 3000 years. The age-frequency distribution (AFD) for all shells (not shown) is strongly right-skewed, with a median shell age of 922 years (Table 3.2). When considered separately, the two species show generally similar patterns. AFDs for bivalves and brachiopods are each right-skewed (not shown), and their medians, standard deviations, and semi-quartile ranges are closely comparable (Table 3.2). Consideration of each site and species separately (Fig. 3.2) indicates that three of the four individual age-frequency distributions exhibit a strongly right-skewed shape and are significantly different from a normal distribution ($p < 0.05$, Shapiro-Wilk normality test with Bonferroni correction). The sample that is not significantly different from a normal distribution is the 30 m brachiopod sample, which has a platykurtic shape and is multi-modal. As would be expected from the graphical representation (Fig. 3.2), the 30 m brachiopod sample is significantly different from the other samples in terms of median age and overall age structure (Kolmogorov-Smirnov and Wilcoxon test, $p < 0.05$). The other three AFDs are statistically indistinguishable, using the same tests. In addition, the inter-quartile range for each distribution is shown in Figure 3.2. Each of these ranges overlap, but it is obvious that the 30 m brachiopod sample is different from the other three.

Variation in time averaging among the samples can be assessed by visual inspection of the AFDs (Fig. 3.2), and by the analysis of confidence intervals around the SQR values for each sample (Table 3.2; Figure 3.3). Considering the SQR comparisons in Figure 3.3, the 30 m bivalve site is the least time averaged sample, followed closely by the 10 m brachiopod site. The 30 m brachiopod site is the most time averaged, and it is significantly different from two of the sites (10 m brachiopods and 30 m bivalves). Comparisons within each species show a significant difference in time averaging among the brachiopods sites, and no significant difference among the bivalve sites. Comparisons between the species indicate that the degree of time averaging for bivalves and brachiopods at the 30 m site is significantly different, while at the 10 m site the two species show differences in time averaging, but these differences are not significant. One complicating factor is that brachiopods are the most time averaged species at the 30 m site, while bivalves are the most time averaged at the 10 m site. However, when the data for each site is pooled for each species, the differences in time averaging are no longer apparent. Thus, when

sample size (and the power of the test) is increased, bivalves and brachiopods show nearly identical time averaging, as measured by SQR (Fig. 3.3E, F).

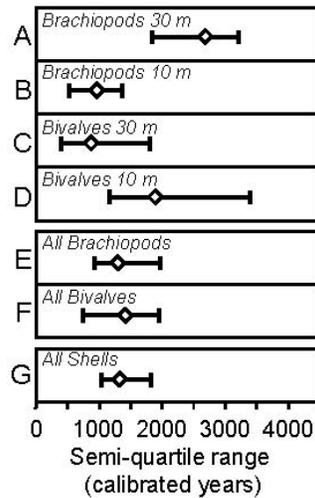


Figure 3.3 - Semi-quartile ranges of each age frequency distribution. A. Brachiopods from the 30 m site. B. Brachiopods from the 10 m site. C. Bivalves from the 30 m site. D. Bivalves from the 10 m site. E. All brachiopods. F. All bivalves. G. Brachiopods and bivalves. 95% confidence intervals were calculated with separate 5000-iteration bootstrap procedures.

Age Structure and Completeness

The mean value from each of the sampling distributions created from the completeness simulations can be considered to be the expected completeness of an average sample with parameters k and r , drawn from a 100% complete record with either a uniform or exponential shape. The expected completeness values for each sample are shown in Table 3.3.

The simulation and random sampling of a uniform distribution has been discussed elsewhere (Kowalewski et al. 1998), but the algorithm used here to model an exponential distribution requires some additional explanation. The exponential variates for this simulation were generated using the *ranexp* function in SAS (v. 9.1), which uses a method based on inverse transform sampling to generate exponentially distributed random variates according to the equation:

$$(5) \quad T = \frac{-\ln U}{\text{lamda}}$$

where T is an exponential random variate, U is a random variate drawn from a uniform distribution on the unit interval (0;1), and $lamda$ is the rate parameter. In principle, values for T range between 0 and infinity, but in practice, T was found to range between 0 and 5 for a rate parameter ($lamda$) equal to 1, which is the default setting for the *ranexp* function in SAS. Since we were interested in generating random shell ages as old as (but not older than) the range for each sample, equation (5) was modified as follows:

$$(6) \quad T_r = r \left(\frac{-\ln U}{lamda} \right)$$

where r is the range of a sample. Instead of the SAS default setting, we used a value of 5 for $lamda$ in each simulation because this made the range of simulated samples very close to the range of the actual sample. This can be shown by Figure 3.4 in which the rate parameter ($lamda$) was varied in a stepwise fashion during successive runs of the model, and the maximum age and the 99th and 95th percentiles of the randomly generated age-frequency distribution was plotted. Using an arbitrary criterion that 99% of the randomly generated ages for any run of the model should be equal to, or less than the range of the sample in question, a rate parameter equal to 5 is the optimal value for each sample.

Once the optimal rate parameter was chosen, the model was run using the parameters for each grouping of the data. Using the sampling distributions obtained from these runs, and a calculated p -value (Table 3.3), we can assess the null hypotheses that the original sample was drawn from a uniform or exponential distribution. In each case, p is the probability of obtaining the original sample by sampling a 100% complete, uniformly or exponentially distributed record. For both distribution types p was calculated as the number of random samples as complete as, or less complete than, the original sample, divided by the total number of random samples. The implications of this method for calculating p are that if the actual completeness is significantly lower than the expected completeness for either distribution type, then that sample was probably not drawn from a 100% complete distribution. On the other hand, if, for example, a sample's completeness value is greater than that expected for an exponential model, then the sample may have been drawn from a 100% complete distribution, but it was probably not an exponential distribution.

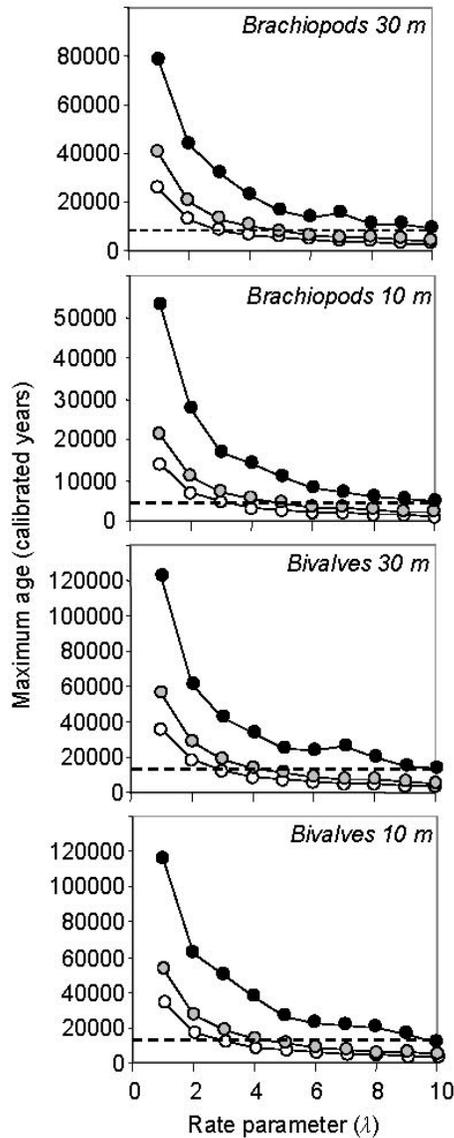


Figure 3.4 - Maximum age (black dots) and the 99th (grey dots) and 95th (white dots) percentiles of each randomly generated age distribution from successive runs of the Monte Carlo model in which the rate parameter (λ) of the exponential distribution was altered in a stepwise fashion. Dotted lines indicate the maximum age of each actual sample.

Figure 3.5 shows the modeled completeness values for each distribution type along with their confidence intervals for each simulation in addition to the observed completeness value for each sample. From Figure 3.5 it can be seen that one of the samples, the 30 m brachiopod sample, most closely resembles what would be expected from a 100% complete uniform distribution (Table 3.3; Fig. 3.5A). Two other samples, the 10 m brachiopod sample and the 30 m bivalve sample, closely resemble the expectation for a 100% complete exponential distribution (Table 3.3; Fig. 3.5B, C). The completeness value for the fourth sample (10 m bivalve) is lower

than what would be expected for either a uniform or an exponentially distributed record (Table 3.3; Fig. 3.5D). The outcome changes somewhat when samples are pooled, as shown in Figure 3.5 E-G. In the case where all shells of a particular species are pooled, the completeness value for both the brachiopod (Fig. 3.5E) and the bivalve sample (Fig. 3.5F) are consistent with the expectation for an exponentially distributed record. The same outcome holds when all samples are pooled (Fig. 3.5G).

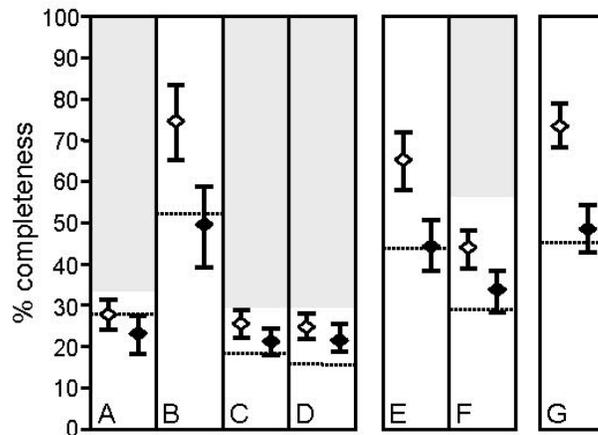


Figure 3.5 - Results of completeness simulations. Filled symbols indicate the mean simulated completeness value from the exponential distribution model. Open symbols indicate the mean simulated completeness value from the uniform distribution model. Dashed lines indicate the actual completeness value for each sample. Shaded areas indicate completeness values that are above the maximum possible completeness for a sample. 95% confidence intervals are the 2.5 and 97.5 percentiles of each completeness distribution. A. Brachiopods from the 30 m site. B. Brachiopods from the 10 m site. C. Bivalves from the 30 m site. D. Bivalves from the 10 m site. E. All brachiopods. F. All bivalves. G. Brachiopods and bivalves. See text for descriptions of each simulation.

Discussion and Implications

Comparisons Between the Two Species and Sites

This goal of this study is to quantify and compare the time averaging of bivalves and brachiopods collected from the same site. These two benthic invertebrate groups are characterized by many physical differences, each of which could play a role in determining the type of time averaged assemblage that is produced. The first major difference is skeletal mineralogy in that (most) bivalves have an aragonitic shell whereas brachiopods are entirely composed of calcite. This would seem to give brachiopods the advantage in surviving post-mortem dissolution, as aragonite is unstable relative to calcite in the modern ocean. In fact, early aragonite dissolution has been implicated in the preferential loss of molluscan material in Paleozoic (Cherns and Wright 2000), Mesozoic (Hendry et al. 1995, 1996; Wright et al. 2003) and modern oceans (Morse et al. 1985). Counteracting this effect somewhat is the fact that brachiopod shells generally have a much higher organic content than bivalves, which may greatly reduce their durability shortly after the death of the organism (Daley 1993). Shell microstructure also differs markedly between brachiopods and bivalves. The shell of *B. rosea* is punctate with two discrete layers, a thin primary layer composed of fine granular calcite, and a thick secondary layer composed of fibrous calcite (Rudwick 1970). The shell of *S. casali* is composed of several layers of crossed-lamellar aragonite. There has been no detailed comparative study of these two shell structures, in terms strength or durability, so it is difficult to assess which of them, if any, would increase the post-mortem survival rate of shells. An additional physical difference between these species is skeletal robustness or thickness. *B. rosea* has a much more robust shell (in terms of thickness) than that of *S. casali*, and this could imply that *B. rosea* is much less susceptible to post-mortem skeletal breakage during transport, but again, this hypothesis has not been rigorously tested. Finally, these two species differ notably in their life habit: *B. rosea* is exclusively epifaunal, while *S. casali* is primarily a shallow infaunal organism. These differences in life habit could translate into different time averaging signatures because infaunal organisms might be more easily buried and less subject to the physical reworking and transport that can occur at the sediment-water interface.

Their physical differences notwithstanding, we report here that brachiopods and bivalves can show very similar magnitude of time averaging when collected from the same site or at least the same region. This suggests that within a single depositional system brachiopods and bivalves

may experience very similar time averaging magnitudes, but that there may be significant differences between any two sites within that system. These site to site differences may be attributable to stochastic variation in any number of taphonomic processes, as recent computer models suggest (Olszewski 2004). They may also result from the dispersal patterns of the organisms themselves. Brachiopods in general (Lee 1991), and *Bouchardia rosea* in particular (Kowalewski et al. 2002), are known to be organized into populations that are ephemeral on ecological times scales resulting in highly patchy distributions at any given time. For example, close inspection of the age-frequency distributions in Figure 3.2 shows that the 30 m brachiopod site would more closely resemble the other sites if the youngest age bins were populated by more brachiopods at that site. Presumably, this paucity of young brachiopods at the 30 m site can be attributed to a lack of a living brachiopod population at this site for the last several hundred years. In turn, this patchy distribution of living brachiopod populations may be attributed to a number of physical parameters such as fluctuating bottom currents, temperature gradients, or intermittent shelf-break upwelling (Campos et al. 2000; Kowalewski et al. 2002).

In addition to their similarity in time averaging magnitude, three of the four age frequency distributions presented here have a very similar right skewed shape reflecting a preferential loss of older shells. This type of distribution has been noted in most previous studies on quantitative time averaging in modern environments, and has been modeled using exponential decay equations (Olszewski 1999). This similarity of age frequency distribution shapes indicates that on some level, the many different post-mortem processes that affect skeletal assemblages produce similar results. That is to say, the longer a shell is around, the more likely it is to be destroyed by the various processes that contribute to taphonomic destruction (Kidwell and Bosence 1991; Olszewski 1999). The sum total of all of these processes tends to produce age-frequency distributions that are right skewed (Kowalewski and Rimstidt 2003).

The completeness analysis summarized in Figure 3.5 is in general agreement with the findings for time averaging magnitude. There are appreciable differences between brachiopods and bivalves at both sites in terms which type of modeled distribution they resemble. However, when the sites are pooled together these differences are not apparent, and the age distributions for both species closely resemble the expectation for samples drawn from 100% complete, exponential distributions.

Similarity in time averaging signature of brachiopods and bivalves (by indirect comparison) has been noted previously by Carroll et al. (2003), in a study that focused

exclusively on *B. rosea*. This result is contradictory to several recent taphonomic reviews (Kidwell and Bosence 1991; Kowalewski 1996; Martin 1999; Behrensmeier et al. 2000), all of which emphasize the potential impact of intrinsic skeletal characteristics on patterns of time averaging. However, in a recent study, Behrensmeier et al. (2005) showed that of the common shell-producing taxa in the fossil record (bivalves, brachiopods, gastropods), the most common genera are just as likely to be small, thin shelled, and unreinforced as large, thick shelled, and ribbed or folded. To the extent that commonness can indicate a high rate of post-mortem skeletal survivability, this implies that intrinsic shell characteristics and susceptibility to taphonomic destruction may be independent for these groups.

This similarity of time averaging signature between two different organisms has important implications for some of the negative aspects of time averaging including the reduction of the temporal resolution of the fossil record (i.e. Fursich and Aberhan 1990), and the generation of false patterns (i.e. Wilson 1988; Kowalewski 1996a; Bush et al. 2002). The analyses presented here agree with many previous studies focused on the quantification of time averaging patterns in that even single samples, collected to minimize their stratigraphic and temporal span, may be significantly time averaged (Kowalewski et al. 1998). However, it is encouraging to note that this pattern seems to be a general one that does not vary appreciably between different shell-producing species. Thus, the temporal resolution of multi-taxic shell assemblages in the fossil record may depend more on environmental and taphonomic factors than it does on the intrinsic properties of their component organisms. Furthermore, since intrinsic durability seems to play a minor role in dictating the formation of a fossil assemblage, the fidelity of the fossil record with respect to biological parameters such as diversity, morphology and size structure may be rather good, even for less durable shell-producers, as has recently been suggested (Bush et al. 2002; Kowalewski et al. 2003; Krause 2004; Tomasovych 2004).

Comparisons with other regions

The estimates of time averaging presented here are of the same order of magnitude as those reported in other recent empirical studies of time averaging duration for shelled marine invertebrates (Flessa et al. 1993; Meldahl et al. 1997; Kowalewski et al. 1998; Carroll et al. 2003; Kidwell et al. 2005). However, the time averaging durations reported here using SQR are consistently greater than most other studies. One of the reasons for this could be the fact that

several of the studies mentioned above used shell material that was collected from very shallow (<2 m), restricted settings (Flessa et al. 1993; Meldahl et al. 1997; Kowalewski et al. 1998). This suggests that water depth may be an important factor in determining the duration of time averaging of a particular skeletal assemblage.

To investigate the potential relationship between depth and time averaging magnitude, a meta-analysis was conducted using data from this study along with selected data from the following sources (Flessa et al. 1993; Meldahl et al. 1997; Kowalewski et al. 1998; Carroll et al. 2003; Kidwell et al. 2005). We restricted this analysis to samples collected from dominantly siliciclastic settings in light of the differences in time averaging signature between shells from carbonate and siliciclastic settings (Kidwell et al. 2005). Before utilizing the previously published data, the various datasets were culled to make them as comparable as possible. Particularly, we were concerned with the vastly different sample sizes from which some of the published data came. Because we intended to use the dispersion metric SQR to compare these various datasets, it was necessary to determine the minimum threshold sample size that would allow retention of the greatest number of dated specimens and still enable meaningful comparisons. This was accomplished by producing a series of bivariate scatter-plots of depth vs. SQR (Fig. 3.6). Each point in these plots represents a sample which was defined as a single collection of one species from one or several closely related sites (typically we used the sample designation defined in each original publication). Once all specimens were sorted into samples, the samples with the smallest number of specimens were removed from the bivariate scatter-plot in a stepwise fashion. After each removal of part of the data, a least-squares linear regression was calculated for the remaining data and the adjusted r^2 and p -value for these regressions were recorded.

A lower threshold sample size of 4 specimens was chosen using the criteria of reasonably high adjusted r^2 values along with p -values significant at the 0.05 level (Fig. 3.6B). The scatter-plot of age vs. depth for samples with $n > 4$ (Fig. 3.6A), clearly shows that there is a significant, positive correlation between the duration of time averaging of a sample and the depth from which it was collected. This trend is not only significant at a sample size threshold of four; a significant correlation is also obtained for each sample size threshold between 4 and 20 (Fig. 3.6B). To illustrate this, a scatter-plot including only samples with greater than 20 specimens is also included in Figure 3.6C. This regression is significant at a similar level to that of Figure

3.6A, and the least squares regression line has a very similar slope, suggesting that this pattern is very robust.

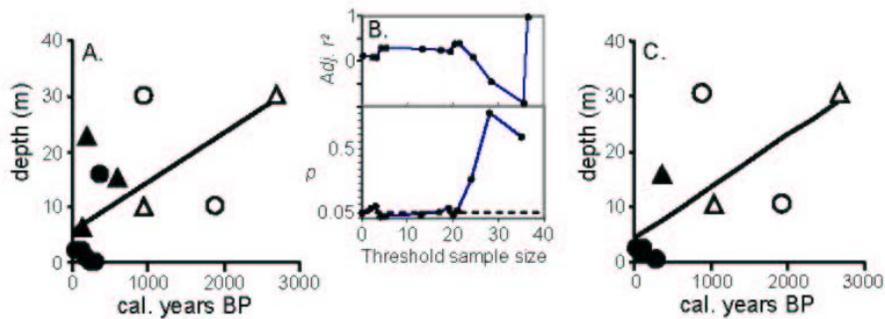


Figure 3.6 - Bivariate scatter-plots of semi-quartile ranges of age distributions vs. depth. A. Scatter-plot of samples using a sample size threshold of $n=4$. B. Adjusted r^2 and p -values for linear regressions considering all possible threshold sample sizes. C. Scatter-plot of samples using a sample size threshold of $n=20$. Open symbols indicate samples from this study, filled symbols are previously published data. Circles indicate bivalve samples, triangles indicate brachiopod samples.

It may be intuitively obvious that shallower samples exhibit a shorter time averaging duration because skeletal debris in such settings may be subject to stronger and more frequent episodes of taphonomic destruction as a result of breakage or abrasion. Also, shallow areas may experience more frequent exhumation events in which buried shells are reintroduced into the taphonomically active zone by storm currents or bioturbation, where they stand a much greater chance of destruction (Martin 1999). However, the strength of the relationship between depth and time averaging suggested by Figure 3.6 is striking, especially considering the fact that the samples considered here come from a rather wide latitudinal range and vastly different depositional and oceanographic settings. Clearly this pattern should be investigated further, and shells from additional depths and depositional settings should be added. The implications of this pattern are that shallow and deep water assemblages may be characterized by fundamentally different temporal resolution regardless of the constituent organisms. This difference may be highly predictable even among a diverse array of depositional settings.

Conclusions

1. Brachiopods and bivalves have a similar time averaging signature when collected from the same depositional setting. This similarity is present when a variety of different metrics are considered, including standard deviation, semi-quartile range and overall shape of the age-frequency distribution.
2. Extrinsic factors such as environment and depth are more important than intrinsic factors such as shell mineralogy, durability, and life habit in determining time averaging magnitude. As a result, the temporal resolution of the fossil record of inherently less durable shell-producing taxa may be much more closely comparable with that of durable taxa than has previously been appreciated.
3. Results of simulations of temporal completeness suggest that shell accumulations from open marine environments may be drawn from underlying distributions that are indistinguishable from 100% complete records. The shapes of these distributions are dictated by the population dynamics for the organism over the time averaged interval, but they need not conform to a simple exponential model. This explains why very old shells can be relatively common at some sites.
4. There is a significant relationship between the time averaging duration of a skeletal assemblage and the water depth at which it accumulated. Deeper assemblages are more likely to have longer time averaging duration than shallow assemblages perhaps because of the increased intensity and frequency of episodes of taphonomic destruction at shallow depths.

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APPENDICES

Appendix 1.1: Raw landmark coordinates – Anterior view

SPECIMEN #	LIVE/DEAD	DEPTH (FATHOMS)	1AX	1AY	2AX	2AY	3AX	3AY	4AX	4AY	5AX	5AY	6AX	6AY	7AX	7AY
B503D	D	20	4.31	9.1	8.75	9.84	15.15	12.41	24.17	10.49	28.35	9.93	16.89	4.57	16.85	17.72
B103D	D	20	2.47	8.17	7.4	9.53	12.65	11.61	20.23	9.66	25.17	7.96	13.84	5.32	12.69	14.71
B502D	D	20	5.41	9.91	9.57	10.65	16.32	13.42	24.89	10.69	28.27	10.22	16.84	6.88	16.45	17.53
B104D	D	20	2.17	11.43	10.16	13.72	14.53	15.58	22.67	12.48	27.09	11.51	14.46	7.17	15.35	19.42
B102D	D	20	3.28	10.74	7.79	11.11	15.66	14.82	23.11	12.59	28.76	11.41	16.71	5.98	16.5	19.16
B106D	D	20	5.09	11.45	12.54	13.27	19.54	15.31	26.08	12.9	31.08	11.77	18.35	7.86	18.04	19.35
B505D	D	20	4.43	9.47	10.61	10.57	16.53	12.63	22.89	10.13	29.47	9.25	16.75	5.53	16.89	17.89
B504D	D	20	3.98	8.87	10.52	10.91	16.45	13.55	22.6	10.48	29.39	8.87	17.01	5.76	17.53	18.31
B105D	D	20	4.32	11.86	7.72	12.4	17.31	16.76	25.62	12.86	29.67	11.9	17.63	7.18	17.4	20.63
B101D	D	20	4.46	12.61	10.77	15.6	19.72	19.45	28.12	15.22	36.58	13.18	19.72	8.24	19.72	24.39
B501D	D	20	7.01	12.16	14.01	13.26	22.64	17.03	31.74	12.39	37.41	12.34	22.12	7.12	21.95	23.86
Y102D	D	25	9.92	18.5	13.2	18.83	22.79	21.45	26.07	20.33	33.59	18.77	20.33	13.26	21.23	27.52
Z104D	D	25	6.33	11.44	11.44	12.4	18.12	15.76	26.55	12.14	30.31	11.22	19.61	6.81	18.91	20.74
Y101D	D	25	10.04	16.84	12.77	16.78	23.75	21.08	32.4	17.17	35.52	17.68	23.47	11.43	22.86	27.1
Z106D	D	25	8.58	10.2	14.91	11.09	20.04	14.02	29.24	11.09	35.94	10.99	21.87	4.97	21.5	21.08
Y103D	D	25	8.63	17.27	12.81	18.1	21.78	22.06	28.91	18.72	35.15	16.99	22.34	13.43	22.34	26.91
Z102D	D	25	9	16.96	10.85	16.1	24.85	20.72	36.14	16.59	39.28	16.9	25.04	11.47	23.81	27.51
Z105D	D	25	6.61	13.54	11.09	14.11	19.64	18.54	29.95	14.43	35.26	14.01	22.08	8.96	19.64	24.58
Z108D	D	25	5.12	13.26	12.95	15.61	22.3	18.22	30.13	15.2	35.87	13.52	24.39	8.25	21.15	24.65
Z103D	D	25	9.07	12.79	15.11	15.58	22.84	20.05	33.54	14.41	36.91	13.37	24.53	8.43	23.66	24.88
Z107D	D	25	8.16	12.19	11.88	13.66	19	18.11	30.61	13.08	35.01	12.77	23.5	7.06	19.94	21.67
C106D	D	30	7.67	11.11	7.67	11.11	20.09	15.03	24.42	13.3	31.25	11.01	20.03	7.77	19.51	18.21
C103D	D	30	8.38	13.62	15.48	15.86	24.24	18.93	33.45	14.71	39.46	13.11	24.82	6.59	24.82	24.31
C105D	D	30	6.01	9.64	14.35	11.86	20.78	13.83	30.62	10.05	35.23	9.48	22.49	3.99	20.1	19.07
C104D	D	30	10.58	15.06	18.14	17.88	27.5	21.22	33.33	18.53	42.63	15.71	27.31	9.1	26.73	26.28
C102D	D	30	9.64	15.57	15.7	18.06	22.85	21.38	34.4	17.3	41.67	15.64	26.61	7.53	25.59	29.23
C101D	D	30	12.05	19.57	20.02	23.84	26.18	26.31	37.45	20.54	41.08	19.89	22.29	12.63	25.72	32.33
D130D	D	35	8.23	4.37	9.3	4.54	11.51	4.99	13.72	4.57	15.02	4.46	12.25	3.28	11.72	6.52
D106D	D	35	6.33	11.15	10	12.02	17.71	14.31	25.87	11.61	28.12	11.1	16.1	8.58	16.93	18.49
D127D	D	35	6.52	9.72	11.07	11.6	16.02	13.65	22.8	11.6	27.66	10.42	15.93	6.35	17.29	17.51
D101D	D	35	4.23	11.36	11.13	13.94	17.42	16.48	25.02	12.49	28.92	11.74	15.96	7.75	16.62	19.72
D128D	D	35	9.07	11.9	14.08	12.79	21.57	15.07	28.41	12.79	31.98	11.85	19.88	8.23	19.79	20.68
K104D	D	35	9.48	12.04	14.24	12.93	20.42	14.92	27.91	12.51	30.73	12.15	20.58	10.26	20.99	18.74
D112D	D	35	6.48	9.11	11.64	10.38	18.07	12.81	25.92	10.07	30.57	9.36	18.98	5.67	18.58	17.31
K105D	D	35	8.41	13.04	13.45	14.08	19.63	15.74	25.4	14.13	30.23	13.09	22.39	10.34	20	20.15
D107D	D	35	4.26	12.13	8.79	12.86	17.62	16.75	25.58	13.14	30.57	12.63	17.76	8.51	17.62	21.78
D122D	D	35	7.3	12.79	15.99	15.08	21.31	17.1	29.68	14.39	33.73	13.37	21.63	8.63	20.89	21.37
D123D	D	35	5.66	14.55	10.42	15.56	20.74	20.42	28.25	16.77	33.81	15.24	22.22	11.16	20.16	24.23
D116D	D	35	6.13	12.46	10.02	13.16	19.29	17.06	28.45	13.11	31.75	12.76	20.86	8.05	18.68	20.25
K107D	D	35	7.9	13.47	14.25	13.58	24.71	17.14	31.33	14.92	36.79	14.19	23.32	8.57	22.21	22.32
D120D	D	35	8.08	15.79	12.31	16.61	22.04	22.29	32.46	16.86	36.69	16.61	25.07	10.42	21.09	26.39
D313D	D	35	8.55	18.59	14.51	19.83	24.04	23.78	31.29	20.54	39.52	18.34	23.97	12.96	24.17	28.57

SPECIMEN #	LIVE/DEAD	DEPTH (FATHOMS)														
			1AX	1AY	2AX	2AY	3AX	3AY	4AX	4AY	5AX	5AY	6AX	6AY	7AX	7AY
D113D	D	35	5.6	9.84	8.48	10.45	18.22	14.08	29.33	10.6	32.76	9.94	18.68	5.75	18.37	19.43
K101D	D	35	5.19	11.55	14.09	13.64	20.81	16.13	31.24	12.21	36.22	11.55	22.44	6.97	21.27	21.52
K103D	D	35	7.98	12.69	11.71	11.04	21.03	13.78	29.32	11.86	33.31	12.59	20.72	7.31	21.14	20.83
D114D	D	35	6.38	12.35	11.24	13.22	19.24	17.16	28.86	12.91	32.86	12.05	19.09	8	18.38	24.1
D109D	D	35	8.62	11.93	12.65	12.93	20.33	17.02	27.18	14.59	33.98	12.32	20.66	8.18	20.66	21.82
D111D	D	35	5.42	14.82	14.94	17.91	21.36	20.83	33.03	15.65	39.63	15.11	22.61	8.87	20.95	25.83
D125D	D	35	10.77	14.94	15.56	17.49	24.77	23.59	35.98	17.37	40.52	15.56	25.71	11.45	25.27	27.07
D124D	D	35	6.84	12.83	11.82	13.36	18.98	16.43	27.99	12.88	32.6	12.67	18.87	8.06	18.82	21.94
D129D	D	35	8.75	15.73	10.68	16.32	23.25	21.78	35.17	16.56	38.28	15.44	22.95	10.68	23.13	26.77
D126D	D	35	10.19	13.69	13.5	13.81	24.93	18.69	35.25	13.5	38.75	13.75	24.56	8.94	24.87	24.25
D105D	D	35	9.91	13.15	14.36	14.36	21.73	18.11	29.23	14.93	35.71	12.65	22.75	7.82	21.54	24.15
D108D	D	35	6.81	13.75	14.04	15.42	21.57	19.3	31.25	15	37.35	13.63	22.53	8.78	22.23	24.38
D312D	D	35	8.86	14.93	12.41	15.45	23.53	20.17	33.94	16.03	36.91	15.71	22.88	9.83	22.37	26.76
D115D	D	35	6.62	12.83	9.7	13.23	19.9	17.37	28.74	14.19	33.43	12.78	19.8	7.78	18.99	23.33
K106D	D	35	8.43	11.78	14.24	13.57	22.4	17.26	32.45	12.85	35.46	12.45	22.4	8.32	22.51	20.61
D110D	D	35	7.61	11.66	12.97	13.3	21.13	17.19	30.49	12.92	33.67	11.93	21.29	7.5	20.58	22.12
D102D	D	35	4.72	10.09	10.7	12.1	17.24	14.91	26.31	11.78	30	10.47	18.83	5.14	18.41	19.44
D104D	D	35	10.38	15.61	17.2	17.32	26.69	20.76	36.82	16.56	39.36	16.05	25.1	10.19	26.05	26.75
D103D	D	35	9.47	14.49	15	15.44	23.71	18.18	33.3	15.25	38.07	15.51	24.21	7.5	24.21	25.87
D117D	D	35	6.21	12.98	11.98	14.36	21.46	17.8	33.77	13.53	37.21	12.92	21.9	8.54	21.74	24.23
D118D	D	35	10.25	14.4	14.21	14.59	25.47	17.8	32.07	15.47	38.68	14.21	24.9	8.43	24.46	26.41
D121D	D	35	10.08	9.89	13.55	11.15	24.39	18.21	37.75	10.97	40.14	10.65	27.23	5.99	23.95	21.74
D119D	D	35	5.09	13.71	10.5	13.39	22.2	18.61	33.02	13.52	38.93	13.58	22.07	6.6	21.7	26.04
K102D	D	35	9.25	14.03	14.72	15.66	24.65	20.75	36.48	15.16	39.56	14.97	24.34	9.5	24.65	27.48
K108D	D	35	8.78	14.47	21.77	19.36	25.42	20.97	35.51	15.46	40.08	15.22	24.8	8.97	25.3	27.15
E327D	D	40	5.69	7.76	8.53	8.13	11.36	8.8	15.59	7.98	17.2	8.01	11.81	5.97	11.33	11.54
E325D	D	40	6.1	6.8	7.71	7.07	10.5	7.65	13.78	7.16	15.81	6.95	11.26	5.55	11.17	9.5
E139D	D	40	6.94	8.43	10.45	9.28	12.06	9.87	15.81	8.87	18.24	8.67	12.56	6.88	12.41	11.48
E143D	D	40	3.88	7.35	7.18	8.36	12.72	10.83	19.87	7.93	22.33	7.18	13.15	3.84	13.19	13.22
E104D	D	40	4.68	9	7.02	9.4	13.71	11.2	18.93	9.83	21.87	8.96	13.44	6.29	13.28	13.81
E316D	D	40	5.51	9.29	7.95	9.52	15.1	11.51	21.26	9.56	25.27	9.41	15.6	6.23	15.1	15.06
E508D	D	40	5.31	9.01	8.6	9.98	15.66	12.04	22.32	9.76	24.6	9.38	15.89	6.32	14.84	15.4
E509D	D	40	4.43	9.43	7.11	10.09	13.21	11.48	17.39	10.34	19.56	9.87	12.58	7.51	12.29	14.4
E326D	D	40	4.52	4.58	6.05	4.64	12.02	6.23	18.04	4.82	19.04	4.67	13.46	2.5	11.75	8.92
E311D	D	40	7.02	10.7	11.25	11.07	18.74	14.42	26.23	11.3	30.32	10.7	18.6	6	18.74	18.28
E309D	D	40	5.94	7.36	11.8	8.97	15.86	10.15	21.95	8.2	25.67	7.82	15.4	3.87	15.71	14.56
E330D	D	40	10.75	18.48	10.75	18.48	22.02	23.05	30.89	18.93	33.92	18.53	22.14	14.87	22.48	26.77
E320D	D	40	5.64	10.81	11.19	11.65	18.27	15.01	28.34	11.56	31.32	11.28	17.85	6.94	18.83	18.32
E324D	D	40	5.56	10.93	11.44	11.16	19.68	13.33	26.48	11.53	32.45	11.02	19.21	6.48	18.7	18.84
E307D	D	40	6.29	14.61	13.93	17.9	21.58	21.35	35.73	16.03	39.24	15.4	22.54	9.23	21.92	25.88
E312D	D	40	9.93	15.47	14.89	15.79	24.69	20.31	36.03	15.99	38.94	15.47	24.37	7.67	25.53	26.49
E506D	D	40	3.28	10.77	8.88	12.56	17.33	15.97	25.43	11.73	30.98	10.42	17.07	6.17	17.77	20.26
E102D	D	40	9.24	18.01	15.95	18.85	22.96	22.42	33.53	17.7	39.7	16.98	25.44	11.42	24.71	27.01
E310D	D	40	9.57	14.75	17.25	17.56	24.14	20.61	35.79	16.03	39.45	15.49	24.45	9.15	23.53	25.79
L101L	L	20	5.29	7.6	8.83	7.66	13.77	8.8	17.34	8.09	19	7.46	12.43	5.86	12.43	10.83
B101L	L	20	7.75	12.84	12.84	13.11	21.19	16.91	26.71	15.01	32.13	12.73	20.75	8.29	20.7	21.73

SPECIMEN #	LIVE/DEAD	DEPTH (FATHOMS)														
			1AX	1AY	2AX	2AY	3AX	3AY	4AX	4AY	5AX	5AY	6AX	6AY	7AX	7AY
B107L	L	20	6.78	14.87	11.57	15.83	23.15	21.29	35.62	15.89	40.11	15.17	24.34	9.77	22.55	26.56
B103L	L	20	7.58	15.48	16.62	18.66	23.31	22.55	34.58	17.26	38.91	15.99	24.65	10.38	23.06	26.56
B102L	L	20	8.29	11.54	10.79	11.22	20.87	15.88	32.41	11.76	34.74	11.71	22.44	6.83	22.17	21.03
B106L	L	20	10.34	16.92	15.3	18.1	25.71	22.17	33.77	19.88	44.85	17.44	27.86	8.94	26.01	30.66
B109L	L	20	6.46	14.31	12.86	16.42	22.51	20.1	31.93	16.78	37.54	15.09	21.79	9.66	22.39	26.38
B108L	L	20	4.87	14.96	10.88	17.49	23.07	23.31	30.28	19.47	40.08	15.02	22.65	10.09	21.75	27.7
B104L	L	20	7.81	17.52	14.85	18.98	23.61	22.98	31.68	19.81	39.87	17.33	25.07	11.49	23.11	28.63
B105L	L	20	7.34	14.36	13.79	16.08	23.17	20.81	32.68	16.79	41.49	14.62	24.45	8.62	24.32	27.89
Z109L	L	25	4.24	10.24	9.36	11.16	17.15	14.61	23.19	12.21	29.66	10.98	16.58	6.87	17.11	19.03
Z101L	L	25	6.44	8.24	10.94	8.92	17.72	12.31	24.76	9.01	27.55	8.11	17.55	4.46	17.55	15.32
Z106L	L	25	4.35	9.43	10.02	9.89	16.05	12.93	24.31	9.43	30.61	8.21	17.69	3.67	16.51	18.1
Z107L	L	25	9.27	15.64	16.13	17.33	23.35	21.66	34.54	16.01	37.49	15.52	24.01	9.39	23.29	26.48
Z108L	L	25	8.81	12.65	14.27	14	22	17.03	30.54	13.84	35.84	12.38	23.03	6.27	22.7	23.35
Z105L	L	25	5.51	11.92	10.34	12.82	16.75	16.43	26.23	12.19	28.98	12.05	17.38	5.24	16.79	22.62
C101L	L	30	6.44	7.72	10.21	8.59	12.12	9.1	14.13	8.59	16.43	7.86	12.03	6.21	11.73	10.91
D116L	L	35	7.37	8.14	9.83	8.66	11.58	9.06	14.13	8.39	15.36	8.08	11.4	6.76	11.37	10.17
D110L	L	35	6.13	6.67	7.68	7.34	10.97	8.32	14.96	7.28	16.58	6.7	11.31	4.91	11.31	10.06
D115L	L	35	6.35	8.97	8.61	9.51	11.62	10.26	14.51	9.57	16.83	9.03	12.07	7.37	11.5	12.01
D107L	L	35	5.4	7.19	8.19	8.25	11.19	8.96	15.04	8	17.27	7.26	11.75	5.46	11.1	10.88
D108L	L	35	3.88	8.14	7.17	9.25	11.27	11.12	16.77	9.19	19.1	8.32	12.39	6.3	11.34	12.52
D109L	L	35	5.82	7.31	8.41	8.35	11.24	9.39	15.86	7.93	17.86	7.51	12.29	5.67	11.21	11.18
D113L	L	35	3.88	9.3	8.02	11.14	13.92	13.41	18.53	11.1	23.26	9.96	13.85	7.07	13.66	16.04
D111L	L	35	4.94	10.08	8.11	11.16	13.98	13.94	19.96	11.43	23.82	10.27	14.09	7.64	14.79	15.98
D102L	L	35	3.08	10.69	7.17	11.52	13.48	14.06	20.25	11.63	23.08	10.72	14.17	6.67	14.78	16.92
D446L	L	35	6.68	12.14	9.57	13.45	17.52	17.16	26.19	13.18	28.49	12.28	18.78	8.62	17.25	19.55
D114L	L	35	6.47	12.45	14.3	15.61	18.87	17.52	26.3	15.46	33.12	12.05	19.47	8.83	18.97	21.53
D103L	L	35	6.92	12.83	12.98	15.66	19.19	18.43	26.62	14.85	32.07	13.03	19.7	8.54	18.84	22.37
D449L	L	35	4.9	13.23	14.87	17.55	20.61	20.03	33.58	15.34	36	14.92	19.87	8.38	19.45	24.25
D105L	L	35	7.34	11.9	13.22	14.18	19.29	17.42	26.78	13.97	33.47	12.61	20.15	6.89	19.39	22.03
D442L	L	35	7.29	14.35	10.96	14.4	22.26	20.45	30.9	16.55	36.6	14.01	22.76	8.02	22.31	24.91
D445L	L	35	9.06	13.79	12.94	15.19	22.57	20.2	29.1	16.77	34.55	14.24	21.89	9.17	22.62	24.26
D112L	L	35	5.66	12.6	9.2	13.98	18.77	18.05	28.33	13.98	32.7	12.75	19.9	8.64	18.97	20.92
D447L	L	35	8.05	12.58	13.42	14.16	20.89	17.84	29.79	14.1	34.1	12.84	21.32	8.79	21.37	21.63
D443L	L	35	7.41	13.65	12.64	15.05	20.56	18.26	28.54	15.17	34.21	13.65	20.56	9.32	21.35	22.64
D452L	L	35	8.48	13.42	15.11	16.29	21.23	19.15	29.03	15.89	36.56	14.15	24.88	8.82	21.4	23.36
D440L	L	35	6.01	14.21	10.9	15.17	20.56	21.68	32.8	15.67	36.12	14.55	24.15	8.09	21.35	25.39
D106L	L	35	6.46	10.23	8.96	10.79	18.63	15.88	29.57	10.43	32.27	9.77	20.41	5.5	19.14	19.29
D104L	L	35	7.11	12.13	14.52	15.13	20.56	17.46	26.29	15.08	34.77	11.93	21.27	7.82	20.81	21.37
D441L	L	35	6.4	14.55	11.97	15.62	23.48	22.3	36.01	15.62	41.01	14.49	23.2	9.1	22.92	25.28
D450L	L	35	10.04	16.31	16.05	17.14	28.21	21.36	37.42	16.44	40.49	15.61	23.47	7.48	25.65	26.86
D448L	L	35	6.04	13.44	13.28	15.54	20.42	18.32	27.34	15.8	33.75	13.59	20.21	8.19	19.73	22.31
D101L	L	35	6.31	14.22	11.07	16.15	19.68	20.75	31.82	14.92	33.69	14.55	20.16	9.52	19.89	25.08
D517L	L	35	7.73	14.35	15.78	17.92	25	23.18	35.78	17.27	43.24	14.67	24.67	8.05	24.22	28.89
E144L	L	40	6.08	6.49	9.3	7.87	12.05	8.6	15.32	7.37	17.22	6.64	11.55	4.71	11.52	9.68
E141L	L	40	6.81	7.77	8.75	8.37	12.17	9.1	15.42	8.17	16.58	7.97	11.97	6.17	11.45	10.9
E143L	L	40	7.57	6.65	10	7.33	11.72	7.63	14.18	7.12	16.05	6.85	12.14	5.58	11.63	8.99

SPECIMEN #	LIVE/DEAD	DEPTH (FATHOMS)														
			1AX	1AY	2AX	2AY	3AX	3AY	4AX	4AY	5AX	5AY	6AX	6AY	7AX	7AY
E114L	L	40	2.72	6.63	6.76	7.92	9.41	8.91	15.05	7	17.3	6.73	10.2	4.33	9.65	10.3
E145L	L	40	6.88	7.2	8.54	7.69	11.37	8.1	14.08	7.66	16.29	7.2	11.45	5.65	11.42	9.65
E146L	L	40	6.07	7.63	9.58	8.76	11.38	9.29	15.14	8.39	17.6	7.8	11.95	5.82	11.47	11.27
E142L	L	40	5.47	5.5	8.56	6.61	11.35	7.37	16.24	5.88	17.32	5.71	11.88	3.7	11.32	9.52
E127L	L	40	3.74	8.52	9.14	9.92	14.82	12.65	18.99	10.7	25.95	9.3	14.16	5.49	15.14	15.52
E117L	L	40	4.57	9.24	9.17	9.53	14.77	10.95	19.55	9.6	24.33	9.17	14.84	5.42	13.92	13.84
E107L	L	40	7.36	8.26	9.91	9.34	13.02	10.45	17.03	8.92	18.41	8.38	13.62	6.35	12.84	11.53
E133L	L	40	5.26	8.75	8.68	10.11	13.53	13.01	21.4	10.11	24.01	9.67	16.65	6.25	12.94	14.67
E119L	L	40	3.79	6.85	5.97	7.84	9.74	9.05	14.87	7.69	16.2	6.95	10.72	4.51	9.79	10.74
E135L	L	40	1.91	8.15	5.69	9.97	10.03	11.3	15.69	9.6	19.51	8.18	10.81	5.35	9.97	13.15
E129L	L	40	4.35	8.91	8.47	10.78	12.52	12.55	18.74	10.44	21.7	9.86	13.5	6.94	13.37	14.22
E118L	L	40	2.92	8.02	6.52	9	11.5	10.38	15.42	9.06	20.37	7.65	11.82	4.95	11.25	12.79
E131L	L	40	3.65	8.87	10.11	10.84	14.74	12.66	19.01	11.2	27.01	9.09	16.13	5.62	14.49	16.71
E132L	L	40	3.54	9.11	8.63	10.44	15.53	12.36	21.44	10.22	25.46	9.11	13.69	5.65	14.58	15.65
E102L	L	40	4.62	12.06	6.43	12.94	17.77	16.47	22.52	14.12	28.49	11.6	17.82	8.32	16.76	19.87
E136L	L	40	6.89	11.55	10.23	12.78	17.12	15.8	26.57	12.47	28.9	11.55	18.26	7.35	18.22	19.86
E138L	L	40	4.3	8.44	8.59	10.42	13.19	12.2	19.2	9.77	23.83	8.59	15.02	5.28	13.49	14.71
E120L	L	40	4.41	10	8.11	11.63	15.92	14.37	20.55	12.18	25.37	10.93	15.63	7.22	14.44	17.07
E116L	L	40	10.55	13.03	15.41	14.67	22.8	16.89	31.29	13.19	34.14	12.45	21.95	7.44	21.16	22.06
E128L	L	40	6.95	12.75	12.36	14.97	18.88	17.24	26.9	13.57	31.19	12.27	18.88	8.16	19.07	21.83
E122L	L	40	6.02	15.16	10.16	15.75	19.95	20.97	28.12	16.51	36.02	15	20.59	9.3	20.7	25.81
E124L	L	40	5.63	11.88	12.77	14.69	18.78	16.38	26.29	13.38	32.39	10.75	18.54	6.43	18.5	20.8
E110L	L	40	8.01	12.61	12.27	13.92	22.33	17.1	33.07	12.56	35.17	11.76	21.25	5.62	21.08	22.84
E108L	L	40	6.78	9.39	9.65	10.5	18.74	15.52	27.93	10.85	32.66	9.39	16.38	4.07	18.79	19.59
E104L	L	40	6.17	13.34	11.85	14.72	20.04	18.29	28.7	14.14	33.27	12.97	20.04	7.02	20.31	23.71
E103L	L	40	4.7	11.39	8.91	12.82	16.58	16.19	27.47	12.62	30.99	11.93	19.65	5.89	17.47	21.73
E123L	L	40	8.05	17.52	11.76	17.02	28.85	23.28	38.32	17.27	43.46	16.71	25.63	9.53	26.49	29.78
E101L	L	40	7.75	14.04	9.55	14.91	24.17	21.2	34.25	16.66	40.02	13.46	24	8.85	25.16	24.64
E125L	L	40	5.67	14.61	13.17	18.06	22.06	22.5	31.28	17.39	38.56	14.5	21.33	9.44	22.33	27.83
E130L	L	40	6.05	13.28	12.35	15.22	19.22	18.25	27.22	14.61	32.96	12.97	19.68	8.25	20.09	21.99
E109L	L	40	5.07	12.08	11	12.48	22.06	18.18	32.94	12.77	38.24	12.03	20.57	6.21	21.77	25.59
E112L	L	40	8.84	16.09	17.15	18.82	24.93	23.6	35.17	19.68	41.89	17.75	25.27	6.78	26.46	28.26
E121L	L	40	4.83	10.85	13.28	13.98	19.25	16.07	27.41	12.84	34.08	10.05	20.25	5.17	18.41	20.95
E105L	L	40	7.09	14.5	15.94	17.32	22.59	20.02	33.45	15.5	40.1	15.5	24.35	7.09	22.72	26.99
E111L	L	40	2.55	10.41	8.18	11.73	15.41	14.82	24.18	11	28.45	10.45	15.91	5.32	15.64	18.73
E106L	L	40	5.34	13.87	9.21	14.32	17.69	18.03	27.86	14.21	32.18	13.37	18.2	7.98	18.14	24.15
E113L	L	40	8.91	12.87	16.57	15.71	25.15	21.32	36.23	15.84	42.37	14.39	25.28	6.01	25.01	25.81
E134L	L	40	7.69	15.78	13.47	18.38	22.66	22.89	36.88	15.49	38.67	15.61	23.58	8.32	22.72	27.98

Appendix 1.2: Raw Landmark coordinates – Dorsal view

SPECIMEN #	LIVE/DEAD	DEPTH (FATHOMS)	1DX	1DY	2DX	2DY	3DX	3DY	4DX	4DY	5DX	5DY	6DX	6DY	7DX	7DY	8DX	8DY	9DX	9DY
B503D	D	20	17.56	1.2	16.04	3.82	18.49	3.73	17.29	4.4	7.29	8.18	26.89	8.13	4.8	13.33	28.93	12.4	18.31	23.38
B103D	D	20	14.25	0.99	12.38	3.87	15.25	4.04	13.79	3.94	4.65	6.77	21.63	5.85	2.66	10.78	25.39	10.11	14.4	19.57
B502D	D	20	16.16	2.14	15	4.78	18.62	4.87	16.65	5.04	8.71	7.77	25.18	7.63	5.04	12.5	28.35	12.14	17.14	21.88
B104D	D	20	17.4	1.24	12.98	3.91	16.05	3.37	15.35	3.53	5.08	8.1	26.9	9.92	3.06	12.64	27.75	13.29	16.67	21.2
B102D	D	20	16.26	0.89	16.04	4.72	17.32	4.81	16.6	4.77	6.94	7.91	26.89	8.09	3.19	12.98	28.98	13.91	16.04	22.64
B106D	D	20	18.15	1.76	17.41	4.07	19.03	4.12	18.56	4.77	9.49	7.55	28.66	8.75	4.72	12.08	30.83	14.81	17.18	24.21
B505D	D	20	17.02	0.8	15.95	3.91	19.69	4.04	18.04	4.27	8.18	7.51	29.86	9.55	5.29	12.8	30.84	13.87	16.09	23.33
B504D	D	20	17.61	0.71	15.97	4.29	20.04	5.09	17.56	4.25	6.59	8.45	27.21	8.18	4.2	12.61	30.22	13.27	15.31	24.11
B105D	D	20	16.87	1.75	16.68	4.15	19.31	4.52	18.48	4.52	8.43	8.85	27.47	8.34	5.58	16.64	30.97	14.52	18.06	25.67
B101D	D	20	22.23	0.78	19.89	4.41	23.97	3.52	22.29	4.58	9.33	9.55	32.12	7.6	6.37	16.26	38.38	15.98	22.23	29.83
B501D	D	20	22.81	1.7	21.7	6.67	23.74	6.61	22.57	7.19	10.41	11.58	34.8	11.64	7.37	18.77	37.95	17.66	19.59	32.92
Y102D	D	25	20.89	5.14	20.28	7.99	24.19	7.32	23.35	7.76	13.24	12.18	32.57	12.23	10.61	16.31	34.19	19.5	23.8	26.7
Z104D	D	25	16.65	3	16.08	5.81	21.1	6.48	18.11	5.95	8.19	8.94	26.17	8.02	5.29	12.73	29.47	13.44	17.75	23.57
Y101D	D	25	23.98	2.98	22.24	6.23	25.05	6.12	23.31	6.52	11.96	11.91	35.16	11.57	10.73	15.73	36.12	14.94	20	27.13
Z106D	D	25	22.3	1.43	19.98	4.97	22.3	5.18	21.77	5.5	11.2	8.4	32.61	10.46	7.29	15.38	35.04	17.71	18.02	27.85
Y103D	D	25	20.73	4.87	19.89	8.07	23.86	7.73	21.17	7.73	12.27	11.15	33.83	12.21	8.29	15.18	35.4	15.63	22.91	27.95
Z102D	D	25	24.17	4.23	21.6	7.36	25.89	7.42	23.93	7.3	9.51	11.9	35.21	10.37	8.59	15.89	38.83	16.07	20.37	30.8
Z105D	D	25	25.96	5.26	23.85	9.04	27.63	8.91	26.02	9.04	16.22	12.56	35.77	11.99	11.54	18.97	40.51	20.7	26.15	32.37
Z108D	D	25	19.63	1.06	17.67	5.45	21.27	4.44	21	5.03	8.94	9.36	30.1	8.62	4.07	16.72	34.81	15.55	21.32	28.09
Z103D	D	25	24.24	2.32	20.92	6.45	25.17	5.52	24.18	5.99	12.26	9.88	35.51	10.17	9.3	17.09	36.62	13.78	23.19	28.19
Z107D	D	25	21.3	1.26	18.95	5.81	21.98	5.86	19.78	6.12	11.25	9.05	29.2	8.06	7.38	15.65	34.49	15.96	20.73	26.69
C106D	D	30	19.99	4.44	18.88	6.77	21.85	6.45	20.42	6.72	11.21	8.94	27.98	8.41	8.2	12.64	31.95	14.28	18.88	22.8
C103D	D	30	24.74	3.59	22.88	5.9	27.44	6.54	23.78	6.35	12.88	10.13	36.28	10.71	8.53	16.73	39.74	17.18	24.29	31.03
C105D	D	30	21.69	2.28	18.78	5.87	23.33	6.24	20.95	6.08	9.26	10.53	34.29	11.01	6.08	15.98	35.77	16.46	22.49	27.3
C104D	D	30	25.61	3.23	23.1	6.77	27.68	7.16	26.13	7.87	10.77	12.45	40.13	13.74	9.1	17.68	40.9	17.74	29.48	29.68
C102D	D	30	26.52	1.94	24.06	6.77	28.58	7.03	26.58	7.48	12.26	12.32	38.52	10.52	9.94	18.97	42.13	19.68	25.74	32.84
C101D	D	30	24.85	2.93	20.75	7.29	26.67	6.25	24.92	6.83	12.23	10.34	36.49	12.03	10.28	16.85	39.81	18.93	24.79	31.62
D130D	D	35	10.43	2.18	9.95	3.65	11.6	3.53	11.19	3.62	7.75	4.98	13.7	4.59	7.22	6.3	14.05	6.1	9.84	9.22
D106D	D	35	17.48	2.9	16.91	5.14	18.83	5.05	18.04	5.61	9.16	8.83	25.42	8.32	6.73	13.46	28.69	13.27	17.24	22.71
D127D	D	35	17.21	1.42	16.5	4.16	18.49	4.25	17.07	4.16	9.38	6.68	25.57	7.48	6.41	11.68	27.69	11.9	18	21.76
D101D	D	35	19.33	1.53	17.28	4.68	19.19	4.15	19.19	4.53	9.59	8.16	29.07	8.83	6.35	12.89	31.41	14.46	16.99	23.25
D128D	D	35	20.79	1.76	19.18	4.43	21.44	4.98	19.98	4.73	11.98	8	27.33	8	8.46	15.3	31.21	14.09	21.34	25.02
K104D	D	35	20.32	4.95	18.16	7.74	21.63	7.74	20.21	7.32	11.84	9.63	27.47	9.37	9.37	12.16	30.74	12.21	19.63	20.63
D112D	D	35	19.39	2.81	16.93	6.39	20.05	5.22	19.03	5.73	10.13	8.29	27.67	8.7	6.8	14.58	31.15	13.61	19.23	23.84
K105D	D	35	20.83	3.74	19.41	6.7	23.1	6.96	21.04	6.7	11.34	9.02	29.27	9.18	9.07	13.08	31.06	14.45	18.25	24.31
D107D	D	35	18.19	1.34	17.59	3.47	19.58	3.66	18.47	3.89	9.07	6.71	28.05	7.59	4.3	15.14	30.6	14.35	17.87	24.81
D122D	D	35	20.43	3.26	19.09	5.94	20.69	5.78	20.21	6.31	11.28	9.14	30.53	9.89	6.68	15.13	33.48	14.12	20.37	25.03
D123D	D	35	20.21	2.57	19.79	4.49	21.5	4.97	21.23	6.1	9.79	9.14	31.44	9.09	6.1	17.43	34.12	15.45	17.43	27.86
D116D	D	35	19.3	3.34	17.4	5.6	20.58	5.44	18.89	6.21	9.7	8.42	29.62	9.6	5.7	13.91	31.78	14.89	19.3	24.74
K107D	D	35	21.96	1.45	19.5	4.47	21.73	4.08	21.73	4.86	14.58	6.87	30.73	7.99	6.48	15.08	36.15	15.64	21.84	28.27
D120D	D	35	23.55	5.04	21.25	8.11	23.87	8.11	23.3	8.3	12	12.06	33.57	12.38	8.62	19.27	37.4	18.89	25.08	31.08

SPECIMEN #	LIVE/DEAD	DEPTH (FATHOMS)																		
			1DX	1DY	2DX	2DY	3DX	3DY	4DX	4DY	5DX	5DY	6DX	6DY	7DX	7DY	8DX	8DY	9DX	9DY
D313D	D	35	23.4	2.8	25.17	5.61	26.47	5.8	25.75	6.06	13.82	9.13	38.46	10.17	9.65	15.78	40.94	15.26	24.32	28.69
D113D	D	35	18.51	1.8	17.89	4.79	20.67	4.74	19.12	5.41	8.04	10.52	30.26	9.64	5.98	15.05	33.4	15.31	16.96	25.72
K101D	D	35	20.78	2.14	19.48	4.9	22.81	4.9	21.88	5.1	6.56	9.79	34.01	8.96	5.21	13.18	36.46	14.69	18.91	26.88
K103D	D	35	20.89	1.82	18.8	5.42	21.2	4.58	20.42	5.57	10.63	8.75	29.22	9.69	6.88	14.9	32.24	17.24	21.51	26.09
D114D	D	35	19.29	1.43	17.76	5.05	19.85	5.36	19.18	5.46	8.83	8.32	29.74	9.64	5.2	15.36	32.76	15.51	18.01	26.89
D109D	D	35	21.78	3.23	18.89	6.13	22.45	5.85	21	6.57	9.42	11.75	28.3	9.08	8.02	15.1	34.04	15.38	20.17	26.13
D111D	D	35	23.67	2.95	20.96	5.24	25	5.54	23.97	6.02	10.84	9.64	37.77	12.11	5.6	17.65	40.78	16.63	25.06	32.59
D125D	D	35	26.11	2.95	24.41	7.03	26.17	7.03	25.1	7.15	13.37	10.29	37.91	11.55	9.73	15.94	40.04	16.44	24.1	29.75
D124D	D	35	20.64	2.51	18.98	5.78	22.62	5.51	20.48	6.74	10.16	12.41	32.25	12.67	8.5	16.84	34.28	17.33	21.18	26.95
D129D	D	35	21.83	3.31	23.02	5.62	26.57	5.68	24.14	5.92	13.02	9.59	35.03	9.7	8.82	17.75	38.46	17.22	20.3	30.35
D126D	D	35	24.46	4.02	24.59	7.11	27.86	7.8	25.47	7.61	14.28	11.01	37.54	12.01	11.13	19.31	40.25	16.67	23.9	31
D105D	D	35	22.45	3.71	21.68	8	24.24	7.93	22.45	7.93	12.47	12.15	34.35	12.54	9.53	19.13	36.72	17.97	23.16	29.55
D108D	D	35	21.76	3.73	20.74	7.09	24.65	7.39	22.12	7.39	9.56	10.94	35.95	11	7.03	16.17	38.72	15.39	23.87	28.56
D312D	D	35	22.96	4.58	24.64	6.97	27.8	7.55	25.35	7.74	12.9	13.48	34	10.64	11.22	19.35	39.61	18.97	21.55	33.09
D115D	D	35	18.77	2.05	17.28	5.74	21.07	6.26	19.53	6	9.43	8.31	29.53	9.38	5.54	16.1	32.45	15.69	17.89	27.17
K106D	D	35	24.22	4.11	21.3	8.06	25.18	7.66	23.04	8.11	15.15	9.46	33.86	10.65	9.24	15.66	36.39	14.31	19.94	26.08
D110D	D	35	21.28	2	19.89	5.17	24.28	5.78	22	6.28	10.44	10.22	32.77	10.22	8.39	15.72	35.94	16.39	21.39	28.94
D102D	D	35	19.42	1	17.19	4.38	21.66	5.48	19.19	4.62	7.86	9.71	27.8	7.95	5.05	15.43	30.95	14.09	14.28	25.19
D104D	D	35	23.78	4.1	22.18	8.33	25.71	8.78	24.55	8.85	13.01	11.99	34.42	12.69	9.42	19.17	38.33	19.94	23.91	32.31
D103D	D	35	24.19	1.98	23.11	6.77	26.36	6.96	24.45	6.77	12.51	11.94	34.79	11.55	9.7	20.74	37.98	20.43	23.55	32.23
D117D	D	35	23.7	1.12	18.54	3.64	24.09	3.47	22.69	3.98	9.19	8.4	33.11	7.51	6.39	14.12	37.59	16.41	24.2	29.13
D118D	D	35	24.94	2.72	23.29	6.52	28.04	7.22	25.13	7.59	12.47	13.73	37.03	13.92	10.44	22.03	39.11	17.72	19.94	33.04
D121D	D	35	23.03	4.16	21.88	8.76	26.87	8.06	24.75	8.44	12.66	11.9	35.82	11.58	9.34	17.78	39.59	17.59	24.24	30
D119D	D	35	24.43	2.53	22.47	7.66	26.2	7.78	25.13	7.91	9.62	12.66	38.29	11.84	7.59	19.05	41.14	19.49	24.3	32.28
K102D	D	35	24.67	2.6	22.33	7.36	26.7	7.04	22.71	7.61	11.35	11.67	36.22	11.16	8.63	18.27	38.88	18.46	22.2	30.19
K108D	D	35	24.34	2.42	21.36	6.96	26.89	6.09	24.28	7.45	11.74	11.86	36.76	12.67	9.13	18.88	40.24	20.37	21.11	31.8
E327D	D	40	12.18	2.25	11.66	3.94	12.92	3.75	12.09	4.03	7.32	5.72	16.18	5.75	6	8.4	17.5	8.27	12.12	13.84
E325D	D	40	13.55	3.85	11.56	4.77	13.27	4.25	12.51	4.89	9.82	5.6	16.02	6.27	7.49	8.68	17.25	9.27	12.35	13.12
E139D	D	40	11.66	2.46	10.58	3.81	12.6	3.43	12.19	3.69	6.8	5.6	16.29	5.42	6.18	7.91	17.55	8.06	11.78	12.07
E143D	D	40	13.02	0.89	11.96	2.34	14.23	2.3	13.23	2.96	5.64	6.12	20.86	6.87	3.57	10.14	22.54	12.03	11.1	18.59
E104D	D	40	13.83	3.15	13.29	5.08	15.42	4.88	14.31	5.22	7.9	7.15	21.02	7.97	5.22	11.25	22.51	11.05	12.88	18
E316D	D	40	15.15	2.15	13.77	4.38	15.88	4.5	14.54	4.54	6.88	6.92	22.96	7.19	5.31	9.5	25.07	9.92	14.5	17.61
E508D	D	40	13.16	1.25	12.05	3.5	14.45	3.12	13.69	3.54	6.62	6.27	20.99	6.77	3.54	10.76	23.57	10.57	12.4	19.32
E509D	D	40	12.18	2.12	10.51	4.39	12.95	3.88	12.5	4.33	7.21	6.19	18.04	6.54	4.55	9.81	19.84	11.31	11.99	16.15
E326D	D	40	11.84	1.23	10.03	3.96	12.57	3.28	12.23	3.62	5.7	5.49	14.96	4.97	3.77	7.79	18.67	8.28	12.39	14.04
E311D	D	40	18.18	1.31	18.18	4.02	19.9	4.25	18.46	4.44	9.72	8.74	25.42	7.38	6.78	14.91	29.76	15.28	16.54	24.39
E309D	D	40	15.21	1.13	12.92	4.44	16.3	4.2	15.1	4.59	5.99	8.33	23.69	7.39	5.37	10.74	25.25	11.2	14.71	20
E330D	D	40	22.97	3.51	21.93	6.79	23.66	6.79	22.79	6.73	13.76	9.38	31.77	10.3	10.59	15.08	34.07	15.43	22.39	25.67
E320D	D	40	19.81	1.57	18.24	4.48	21.67	4.52	19.43	4.67	8.86	7.86	29.28	7.71	5.71	12.76	31.81	13.52	20.38	24.33
E324D	D	40	19	1	17	4.62	20.67	4.24	19.33	4.38	9.33	6.95	27.28	6.67	4.86	12.76	32.43	13.48	19.81	24.24
E307D	D	40	22.74	1.6	21.77	6.29	23.89	6.11	22.46	6.8	9.2	10.23	36.69	11.49	6.11	14.4	39.09	19.71	21.37	30.57
E312D	D	40	26.91	2.06	24.27	6.37	27.42	6.24	25.62	6.57	13.65	10.69	35.47	10.69	10.49	17.51	39.4	18.86	26.91	30.64
E506D	D	40	17.72	1.21	16.16	5.67	19.46	5.44	17.45	5.8	6.96	8.08	29.9	9.1	4.06	13.66	31.51	13.12	16.6	24.99
E102D	D	40	21.82	4.33	20.85	8.23	25.48	7.74	23.16	8.41	10	12.07	34.81	11.09	7.56	17.13	38.4	17.62	20.66	29.81

SPECIMEN #	LIVE/DEAD	DEPTH (FATHOMS)																		
			1DX	1DY	2DX	2DY	3DX	3DY	4DX	4DY	5DX	5DY	6DX	6DY	7DX	7DY	8DX	8DY	9DX	9DY
E310D	D	40	23.11	2.46	21.26	7.44	25.07	7.56	23.17	7.8	10.2	12.41	35.77	11.86	8.11	17.02	38.29	17.02	20.22	29.19
L101L	L	20	11.6	1.42	10.38	3.17	12.53	3.23	11.77	3.72	6.45	5.15	16.57	5.47	4.53	7.12	18.28	8.37	11.8	13.43
B101L	L	20	21.82	1.47	19.98	6.46	23.29	5.37	21.5	6.68	13.03	10.48	31.92	12.43	8.9	16.88	33.55	17.48	23.45	27.63
B107L	L	20	24.37	1.69	24.25	5.02	26.37	5.26	24.98	5.14	10.64	10.46	36.1	9.01	7.38	17.78	40.52	16.99	22.62	30.54
B103L	L	20	25.19	2.88	24.49	6.67	26.41	6.92	25.13	6.79	13.08	10.77	37.24	10.77	8.91	18.85	39.93	17.18	25.06	29.61
B102L	L	20	20.93	1.47	19.51	5.61	22.62	5.61	20.22	5.94	8.99	9.59	32.15	9.37	6.87	13.68	33.46	14.28	22.83	26.87
B106L	L	20	26.05	2.15	26.57	6.38	28.94	6.53	27.46	6.9	13.21	11.95	40	10.46	9.35	20.19	44.97	20.04	26.42	35.99
B109L	L	20	22.48	1.33	21.39	5.58	25.03	5.64	23.45	5.76	8.85	10.36	34.24	9.27	7.45	16.61	38.61	16.55	21.82	31.7
B108L	L	20	24.85	2.36	22.12	6.42	25.64	6.79	23.88	7.33	10.42	10.97	38.12	12.79	5.58	18	41.15	18.06	23.7	30.91
B104L	L	20	24.71	1.87	23.42	7.16	26.65	7.35	24.52	7.16	12.13	11.68	37.29	11.23	8.58	19.03	40.97	18.71	23.61	32.84
B105L	L	20	22.94	2.5	19.74	6.99	26.53	7.75	22.05	6.79	9.29	11.6	34.61	9.68	6.54	18.84	41.08	16.02	21.47	33.2
Z109L	L	25	17.18	1.85	16.56	4.4	18.63	4.49	17.58	4.93	8.06	8.99	25.55	8.55	4.85	13.21	30.35	14.23	19.73	23.79
Z101L	L	25	15.69	2.8	14.53	5.9	17.46	5.47	15.9	5.78	6.34	8.28	24.31	8.32	4.65	11.25	26.34	12.37	16.85	20.69
Z106L	L	25	17.52	0.6	15.96	4.26	18.89	4.4	17.2	3.76	7.2	7.75	27.01	7.84	4.13	12.98	31	13.34	16.33	24.53
Z107L	L	25	22.11	4.36	19.87	8.06	23.45	8.97	21.57	8.85	9.21	14	33.14	11.94	7.94	18.72	36.29	16.96	23.81	30.6
Z108L	L	25	20.32	1.41	18.11	5.95	21.73	5.46	21.35	5.73	9.89	8.49	31.78	11.95	6.16	17.35	32.86	17.46	17.51	27.08
Z105L	L	25	17.4	0.46	14.98	3.56	20	3.56	17.31	4.75	7.17	8.95	28.4	9.27	5.25	13.65	29.36	13.65	17.17	24.84
C101L	L	30	12.52	1.8	11.57	3.38	12.8	3.64	11.91	3.52	7.7	5.16	15.61	5.3	6.13	7.47	16.5	7.53	10.28	11.43
D116L	L	35	11.31	4.38	10.7	5.35	11.85	5.32	11.31	5.5	8.57	6.5	13.92	6.6	7.2	8.54	15.26	8.63	11.09	12.1
D110L	L	35	11.58	2.42	10.8	3.96	12.4	3.78	11.76	4.05	7.92	5.41	15.63	5.84	6.26	8.04	16.81	7.92	11.58	12.76
D115L	L	35	12.37	3.77	11.2	5.19	13.22	4.92	12.37	5.01	7.3	6.91	15.78	5.95	6.55	8.72	17.02	8.39	11.23	12.77
D107L	L	35	11.29	2.49	10.72	4.38	12.18	4.38	11.51	4.26	6.66	6.02	15.74	5.74	5.3	8.14	17.51	7.95	11.32	13.47
D108L	L	35	12.78	1.61	11.65	3.58	13.29	3.64	11.9	3.45	6.46	4.81	17.09	5.22	4.37	7.91	19.59	8.73	11.42	14.78
D109L	L	35	12.39	1.75	11.72	3.38	13.63	3.57	12.42	3.92	7.32	5.99	16.59	5.45	6.5	8.57	18.57	8.53	11.34	13.92
D113L	L	35	14.18	1.04	13.92	3.58	14.96	3.4	14.1	3.69	5.93	6.64	22.24	7.05	3.81	11.34	24.29	10.86	13.21	19.44
D111L	L	35	15.31	1.8	13.67	4.14	16.02	4.34	14.73	4.06	7.34	6.91	21.13	6.95	5.04	11.91	23.91	10.59	14.69	18.67
D102L	L	35	15.55	0.85	13.38	2.87	15.92	3.05	15.37	3.2	6.62	6.43	22.57	7.57	4.26	11.47	24.34	11.84	16.84	20.7
D446L	L	35	18.25	1.54	16.22	3.84	18.88	4.43	17.76	4.29	10.26	6.73	25.93	7.64	6.6	13.1	28.46	12.51	14.82	21.73
D114L	L	35	19.64	2.03	17.06	6.29	21.27	5.43	20.81	5.43	7.66	8.83	28.88	8.53	5.18	13.91	32.64	13.45	18.88	24.97
D103L	L	35	19.02	2.11	17.37	5.67	21.39	6.65	18.4	6.13	8.97	9.74	29.9	10.52	6.34	12.99	31.29	15.05	18.61	25
D449L	L	35	22.22	1.38	19.52	4.71	21.11	4.76	20.37	4.55	6.88	10.79	29.58	7.41	5.19	16.03	35.93	14.66	19.47	27.88
D105L	L	35	20.2	1.68	18.47	5.41	20.82	4.54	20.51	5.26	12.04	8.16	30.36	9.59	7.09	15.46	33.32	15.82	23.06	26.48
D442L	L	35	23.33	1.69	21.86	4.8	25.03	4.69	23.95	5.08	11.19	8.02	34.24	8.14	7.63	14.75	38.08	16.44	22.32	30
D445L	L	35	22.94	1.81	21.07	5.16	23.62	5.33	22.09	5.61	12.63	8.89	31.95	8.67	9.69	16.66	35.12	14.28	20.85	26.97
D112L	L	35	18.64	1.88	17.28	5.43	20.62	4.54	18.95	5.22	8.09	8.67	28.56	8.2	5.22	13.47	32.06	15.51	17.65	24.54
D447L	L	35	19.68	1.65	19.36	4.26	22.5	5.11	19.84	4.95	9.57	8.14	30.9	8.46	6.01	14.68	32.98	14.31	18.62	26.17
D443L	L	35	23.8	2.84	21.92	6.53	24.65	6.65	23.29	6.7	12.21	11.13	33.57	10.62	9.71	18.12	36.75	17.49	22.66	28.45
D452L	L	35	23.42	1.13	22.29	4.76	25.35	4.82	23.76	4.82	12.7	7.77	35.22	8.62	10.09	16.11	38.05	15.48	27.28	26.77
D440L	L	35	22.54	1.58	20.5	5.37	24.17	4.74	22.65	5.2	10.34	9.66	35.07	11.01	7.17	15.19	37.11	15.87	24.51	29.54
D106L	L	35	21.4	2.18	19.22	6.22	22.12	6.01	21.5	6.32	9.27	11.19	31.87	10.73	7.51	16.58	34.04	15.96	20.57	26.58
D104L	L	35	20.2	2.19	18.47	6.63	21.12	6.22	20.87	6.28	8.83	9.39	30.41	9.44	5.87	15.36	33.47	14.54	19.69	26.43
D441L	L	35	21.92	1.41	19.89	5.2	24.18	5.25	21.92	5.25	9.21	8.64	35.03	8.53	4.97	15.71	39.38	15.31	20.56	29.04
D450L	L	35	24.9	2.17	24.33	5.67	26.5	6.88	25.03	7.96	17.01	9.3	33.69	10.19	9.49	19.3	39.81	17.96	21.4	32.93
D448L	L	35	20.42	2.6	18.3	7.27	22.92	6.84	21.75	6.84	8.17	9.6	32.2	10.72	5.46	14.64	33.53	14.43	19.05	25.99

SPECIMEN #	LIVE/DEAD	DEPTH (FATHOMS)																		
			1DX	1DY	2DX	2DY	3DX	3DY	4DX	4DY	5DX	5DY	6DX	6DY	7DX	7DY	8DX	8DY	9DX	9DY
D101L	L	35	22.6	1.69	20.45	6.55	25.2	6.55	23.84	7.12	11.41	11.58	34.01	12.2	7.68	17.91	36.72	17.97	21.81	30.51
D517L	L	35	25.81	2.48	23.46	8.63	27.51	8.63	25.61	8.76	11.63	11.5	40.84	13.46	8.1	18.43	43.78	20.52	29.14	32.61
E144L	L	40	10.75	2.37	9.67	3.66	11.25	3.6	10.61	3.46	6.39	5.07	14.74	5.42	4.86	7.79	15.94	7.76	10.37	12.25
E141L	L	40	11.93	2.33	10.99	3.92	12.55	3.86	12.14	4.01	7.66	5.92	16.03	5.51	6.57	7.99	16.59	7.1	10.9	11.85
E143L	L	40	12.02	1.97	11.04	3.68	12.55	3.56	12.13	3.65	8.54	4.62	15.11	4.68	7.51	6.48	15.96	6.33	11.49	10.31
E114L	L	40	9.1	0.87	8.97	2.15	10.69	2.31	9.85	2.36	4.82	4	14.05	3.67	2.64	8.05	17.26	7.15	11.15	13.08
E145L	L	40	11.8	1.92	10.69	3.29	12.76	3.15	11.48	3.2	8.04	4.75	15.17	4.81	6.76	6.35	16.25	6.67	11.85	10.14
E146L	L	40	11.71	0.71	10.44	2.59	11.97	2.59	11.76	2.59	6.91	4.38	15.44	4.32	5.65	6.29	17.41	7.38	12.26	12.03
E142L	L	40	11.21	0.79	10.72	2.68	12.44	2.71	11.97	2.88	6.38	4.54	15.87	4.66	4.95	6.73	17.33	7.92	10.78	12.26
E127L	L	40	16.1	1.69	14.61	3.86	16.3	3.9	15.71	3.9	7.76	6.1	23.97	6.53	3.58	10.2	26.57	10.87	14.29	19.21
E117L	L	40	13.75	2.13	12.81	4.62	13.86	4.66	13.39	4.69	5.45	6.82	23.07	8.19	3.93	9.6	24.98	10.87	14.91	18.74
E107L	L	40	11.75	1.72	10.81	3.89	12.86	3.77	11.87	3.86	7.14	5.6	15.75	5.33	6.05	7.08	17.2	7.74	11.2	12.41
E133L	L	40	14.53	2.25	13.67	4.27	15.99	4.04	15.43	3.89	7.27	6.67	21.27	6.55	4.46	10.56	24.75	10.26	15.73	18.57
E119L	L	40	10.42	1.11	9.44	2.65	11.67	3.49	10.4	3.07	5.13	4.89	14.47	4.84	3.44	7.91	15.95	7.28	9.13	12.75
E135L	L	40	10.21	1.32	9.97	3.38	11.62	3.76	11.24	3.68	4.06	6.41	17.94	5.94	2.62	9.15	20.32	8.74	12.47	15.32
E129L	L	40	14.37	2.45	13.18	4.44	15.28	4.55	13.57	4.69	7.45	6.64	20.87	7.41	4.48	9.3	22.27	10.38	14.97	16.96
E118L	L	40	12.19	0.45	11.17	2.83	13.34	2.99	12.29	2.99	6.3	4.93	18.62	5.7	2.83	9.07	21.07	9.01	11.87	15.82
E131L	L	40	16.19	1.23	13.58	3.47	15.52	3.51	14.48	3.21	5.04	6.72	23.69	7.31	2.87	11.38	26.49	12.13	17.39	20.52
E132L	L	40	14.74	0.34	12.99	3.1	15.52	3.21	14.22	3.36	5.34	6.57	21.75	5.9	3.17	10.45	25.04	11.98	14.25	21.19
E102L	L	40	16.79	1.65	15.32	4.81	18.23	4.39	16.54	4.98	6.84	8.14	27.05	8.1	4.73	12.53	29.11	11.69	14.26	23.12
E136L	L	40	14.65	3.64	15.62	5.48	18.48	6.22	16.82	5.76	9.49	8.62	25.48	8.66	6.54	13	29.03	13.64	18.8	23.96
E138L	L	40	14.12	2.18	12.18	5.31	15.42	5.23	13.85	5.19	7.4	7.75	21.22	7.75	5.23	12.1	25	12.4	16.26	20.61
E120L	L	40	13.72	1.08	11.82	4.09	15.39	3.46	14.53	4.13	5.28	6.69	21.37	5.69	3.2	10.22	24.09	10.15	13.31	19.44
E116L	L	40	22.55	3.72	20.53	7.07	24.04	7.5	22.34	7.5	12.93	10.53	31.38	11.65	9.95	16.49	33.67	16.6	22.02	27.77
E128L	L	40	18.01	1.5	18.35	3.98	19.76	4.13	19.13	4.61	8.93	7.67	28.59	9.27	6.07	13.59	30.34	14.85	18.98	24.9
E122L	L	40	16.85	1.44	16.8	3.47	18.87	4.19	17.12	4.59	6.44	8.11	27.25	9.23	4.41	11.35	29.05	14.14	15.45	24.28
E124L	L	40	17.66	1.14	17.81	4.09	19.33	4.09	18.38	4.71	9.14	8.09	28.95	8.71	5.48	15.52	32.14	15.62	17.71	25.95
E110L	L	40	22.4	3.2	20.11	5.66	22	6.69	20.86	6.34	12.97	8.97	31.2	9.89	8.23	17.43	35.37	19.71	20.51	29.14
E108L	L	40	18.47	2.09	17.04	4.8	20.15	5	18.16	5.97	9.18	8.42	28.57	8.67	5.56	14.23	31.94	15.51	18.42	25.36
E104L	L	40	20.58	1.49	19.52	4.95	22.55	4.84	21.7	4.84	10.53	7.93	31.7	8.51	8.03	12.13	34.89	17.34	22.18	28.62
E103L	L	40	19.5	0.4	18.86	4.38	20.75	4.58	20	4.58	8.61	9.5	30.65	8.91	6.22	15.97	32.54	13.68	16.47	26.37
E123L	L	40	25.09	1.45	23.77	6.29	25.97	6.23	25.22	6.35	10.44	10.82	39.69	11.07	7.42	20.38	43.21	20.19	21.7	34.28
E101L	L	40	22.23	1.47	20	5.41	24.23	5.35	22.18	5.24	9.71	9.35	33.35	8.47	6.06	16.65	38.35	18.29	21	29.47
E125L	L	40	20.39	0.51	19.33	3.31	23.93	4.27	20.67	3.82	8.99	7.3	32.02	6.52	4.83	15.22	38.26	15.11	23.76	31.24
E130L	L	40	18.8	2.2	17.8	6.02	21.47	6.54	19.74	6.81	8.64	10.31	30.21	10.94	5.97	15.08	33.09	15.92	20.58	26.44
E109L	L	40	22.64	0.8	20.34	3.68	25.17	4.66	21.72	4.31	7.76	9.66	35.4	8.74	5.86	14.77	39.02	17.7	26.32	30.23
E112L	L	40	26.33	1.73	24.8	6.4	29.06	5.53	26.4	6.2	14.13	10.07	40	11.53	9.73	19.6	43.6	18.87	26.4	34.73
E121L	L	40	20.4	0.5	18.4	5.1	22.85	3.9	21.7	4.75	7.8	9.55	29.65	7.5	4.7	15.25	33.55	16.1	18.25	28.3
E105L	L	40	24.49	1.46	23.86	6.27	27.28	6.14	25.82	6.52	13.1	9.68	40.63	13.48	8.99	19.3	42.03	17.22	25.13	33.16
E111L	L	40	18.34	1.84	15.39	6.45	20.05	6.5	18.66	6.22	8.02	8.94	28.71	9.72	5.02	15.25	31.33	15.16	19.54	25.62
E106L	L	40	22.25	1.69	19.99	6.55	24.17	6.89	22.08	6.44	10.79	9.88	32.92	10.73	8.19	17.17	35.35	17.28	22.82	29.25
E113L	L	40	26.42	0.8	23.27	4.75	28.89	4.61	26.28	5.15	14.11	8.49	38.32	9.16	9.3	16.72	43.54	18.19	25.55	33.24
E134L	L	40	22.62	1.16	20.12	6.45	25.58	5.76	24.53	5.93	10.12	9.59	38.08	12.38	7.33	15.93	39.42	15.99	22.62	30.23

Appendix 2.1: Bulk Sample raw data

Ordovician Brachiopods: Bulk Samples (length in mm)										
Alberstadt, 1979				Howe, 1979				Pope, 1979		
<i>Platystrophia annieana</i>	<i>Platystrophia colbienesis</i>	<i>Platystrophia elegantula</i>	<i>Platystrophia ponderosa</i>	<i>Sowerbyella</i> sp.	<i>Rhyncotrema increbescens</i>	<i>Orthorhynchula linneyi</i>	<i>Orthorhynchula sublinneyi</i>	<i>Oepikina minnesotensis</i>	<i>Oepikina minnesotensis</i>	<i>Pionomena recens</i>
9	4.5	10	20.9	4.4	6.2	8.2	9.6	8.62	11.62	2.2
10.3	5.5	10.7	20.2	4.9	6.2	8.5	11.6	8.87	11.62	2.5
11.4	8	11.3	27.7	4.9	6.5	8.5	11.8	9.12	11.87	2.5
8.5	8.5	12	29.1	5	6.8	9.4	13.2	9.12	12.37	3.1
10	8.3	14.2	32.5	5.4	8.3	9.5	13.3	9.37	12.62	3.1
11.3	9	12.8	33.7	5.6	8.3	10.1	14.1	9.87	12.62	3.3
11.7	10	13.1	26	5.8	8.4	10.7	14.5	10.12	12.87	3.3
12.9	11	14	27.5	5.8	8.4	10.9	15	10.37	13.12	3.6
11.9	11	14.7	27.2	5.8	8.9	11	15.3	10.87	13.12	3.8
12.8	11.2	15.7	24.8	5.9	9.5	11.2	15.5	11.12	13.37	3.8
13.4	12.9		28.4		9.5	11.7	16	11.12	13.37	3.9
11.9	14		28.4	5.9	9.5	11.9	16	11.87	13.37	4
11.7	14.1		25.6	6.5	9.8	12.2	16.2	11.87	13.62	4.1
13	13.5		28.8	6.5	10	12.2	16.3	11.87	13.62	4.2
14.4			29.6	6.6	10	12.7	16.4	11.87	13.62	4.2
13			28	6.7	10	12.9	16.6	11.87	13.62	4.2
13.7			28.5	6.9	10	12.9	16.7	11.87	13.87	4.5
13.2			20.4	7.2	10.3	13.7	16.8	12.12	13.87	4.5
12.6			20.5	7.3	10.6	14.1	16.8	12.12	13.87	4.7
13.5			24.8	7.6	11.4	14.1	16.9	12.12	13.87	4.7
			23	7.6	11.4	14.1	17	12.37	13.87	4.9
13.8			19.3	7.7	11.5	14.3	17	12.37	13.87	5
13.5			28.2	8.4	11.8	14.8	17.2	12.62	14	5
14			28.7	8.5	11.9	15.1	17.2	12.62	14	5
15.7			29.5		12	15.5	17.5	12.62	14	5.2
14.4			23		12.1	16.2	18	12.62	14	5.2
16			27.5		12.4	16.4	18	12.87	14	5.2
16.3			17		12.8	17.2	18.1	12.87	14	5.5
17.3			19.4		13.1	18.3	18.2	13.12	14	5.5
15.5			20.7			19.6	18.4	13.12	14	5.5
16.9			30.9			19.8	18.5	13.12	14	5.5
18			27.8			19.9	18.6	13.37	14	5.8
18.5			26			20.7	19	13.87	14.12	6
20.3			23.7			20.9	19	13.87	14.12	6
						21	19.3	13.87	14.12	6.2
						21.5	19.4	14.12	14.12	6.4
						21.6	21.3	14.12	14.12	6.4
						22.1	21.8	14.12	14.12	6.7
							22.3	14.12	14.12	6.9
								14.12	14.12	6.9
								14.12	14.12	6.9
								14.37	14.12	7.2
								14.37	14.12	7.4
								14.37	14.12	7.4
								14.37	14.12	7.4
								14.37	14.37	7.4
								14.87	14.37	7.6
								14.87	14.37	7.8

Silurian Brachiopods: Bulk Samples (length in mm)

Amsden, 1968

<i>Dicoelosia bilobella</i>	<i>Dicoelosia oklahomensis</i>	<i>Antirhynchonella thomasi</i>	<i>Hircinisca havliceki</i>	<i>Eospirifer acutolineatus acutolineatus</i>	<i>Eospirifer acutolineatus pentagonus</i>	<i>Kozlowskiella (K.) vaningeni</i>	<i>Atrypina erugata</i>	<i>Nanospira clarensis</i>	<i>Dicamaropsis parva</i>	<i>Meristina clarensis</i>
1.75	1.6	4.4	5.5	4.5	6.6	4.6	3.1	1.7	1.8	3.7
1.8	1.6	5.8	5.7	4.6	7.2	5.3	3.7	2	3	5.5
1.9	2.5	7.7	5.8	6	8.6	5.3	3.8	2.4	3	5.6
1.9	2.6	7	5.8	7.5	8.7	5.8	3.9	2.6	3.1	5.7
2	2.6	10	5.8	8	8.7	6.2	4	2.8	3.3	6.4
2	2.7	10.3	6	8.2	8.9	6.3	4.3	2.8	3.3	6.9
2.1	2.9	10.7	6	8.7	9.9	6.4	4.3	2.8	3.5	7.5
2.1	3	11	6	9.1	11.3	6.4	4.4	2.8	3.7	7.6
2.1	3.1	11.1	6.1	9.3	11.6	6.4	4.4	2.9	3.9	7.8
2.1	3.1	8	6.6	9.7	11.9	6.7	4.6	3	4.2	8
2.1	3.2	8.3	6.8	9.9	11.9	6.7	4.7	3.2	4.6	8.1
2.3	4	8.5	6.8	10	12.3	6.8	4.7	3.4	4.6	9.2
2.3	5.2	8.7	6.9	10.4	12.3	6.8	5	3.5	4.7	9.5
2.3		9	7	10.4	12.4	6.9	5	3.5	4.7	9.7
2.4		9	7.3	10.8	12.8	6.9	5.1	3.5	4.7	9.9
2.5		9.5	7.3	10.9	13.1	7	5.4	3.5	4.8	10
2.5		9.6	7.4	10.9	15	7.1	5.6	3.7	5	10.8
2.5		10	7.5	11.4	16.4	7.1	5.8	3.8	5	12.8
2.6		10	7.6	11.5	16.5	7.2	7.8	3.8	5	13.6
2.6		10	7.6	11.7	16.5	7.2		3.9	5	15.9
2.75		10.2	7.8	12.2	17.1	7.5		3.9	5	18.2
2.9		10.7	7.9	12.8	17.6	7.8		4	5	
2.9		10.8		19.2	18.2	7.9		4	5	
3		11		14.3	18.7	8.1		4	5	
3		11.2		16.3	18.7	8.2		4	5.1	
3		11.3		17.3	18.9	8.2		4	5.2	
3		11.3		17.5	20	8.3		4.1	5.3	
3		13		17.8	20	8.4		4.1	5.3	
3.1		13.3		19.1	20	8.4		4.1	5.3	
3.1					20.9	8.5		4.2	5.3	
3.2						8.6		4.2	5.3	
3.2						8.7		4.3	5.4	
3.4						8.8		4.4	5.5	
						8.9		4.5	5.5	
						9		4.6	5.5	
						9.1		4.7	5.6	
						9.4		4.8	5.7	
						10.3		4.9	5.8	
						10.6		4.9	5.8	
						10.6		5	5.8	
						10.7		5	5.8	
						10.7		5	6	
						11		5	6	
						11.2		5.1	6	
						11.8		5.3	6	
						12.5		5.6	6	
						12.7		5.8	6.1	

Silurian Brachiopods: Bulk Samples (length in mm)										
Amsden, 1968										
<i>Dicoelosia bifobella</i>	<i>Dicoelosia oklahomensis</i>	<i>Antirhynchonella thomasi</i>	<i>Hircinisca havliceki</i>	<i>Eospirifer acutolineatus acutolineatus</i>	<i>Eospirifer acutolineatus pentagonus</i>	<i>Kozlowskiellina (K.) vaningeni</i>	<i>Atrypina erugata</i>	<i>Nanospira clarensis</i>	<i>Dicamaropsis parva</i>	<i>Meristina clarensis</i>
								5.8	6.1	
								6	6.2	
								6	6.2	
								6.1	6.2	
								6.1	6.2	
								6.2	6.3	
								6.7	6.5	
								6.9	6.7	
								7	6.7	
								7.1	6.8	
								7.2	6.8	
								7.3	6.8	
								7.3	6.9	
								7.4	7	
								7.4	7	
								7.5	7	
								8.2	7	
								8.6	7.1	
								9.5	7.3	
								9.6	7.3	
									7.4	
									7.6	
									7.7	
									7.9	
									8	
									8.1	
									8.1	
									8.1	
									8.2	
									8.2	
									8.3	
									8.4	
									9	
									9	
									9.2	
									9.3	
									9.3	
									9.4	
									9.5	
									9.6	
									9.6	
									9.8	
									10.1	
									10.3	
									10.5	
									10.6	

Devonian Brachiopods: Bulk Samples (length in mm)					Mississippian Brachiopods: Bulk Samples (length in mm)							
Li & Jones, 2003	Balinski, 1995			Balinski, 1997	Gordon et al., 1993							
<i>Nucleospira lens</i>	<i>Biernatella ovalis</i>	<i>Biernatella lentiformis</i>	<i>Biernatella polonica</i>	<i>Waiotrypa sulcarina</i>	<i>Inflatia inflata</i>	<i>Inflatia cherokeensis</i>	<i>Inflatia cooperi</i>	<i>Inflatia clydensis</i>	<i>Inflatia gracilis</i>	<i>Inflatia pusilla</i>	<i>Adairia adairensis</i>	
7	4.6	1.5	5.5	6.4	20.4	16.5	28.2	26.8	14.1	9.3	16.9	
7.4	5.8	1.5	5.6	6.6	22.1	16.8	28.7	27.3	14.2	9.4	17.1	
7.5	6.1	1.6	5.8	6.9	22.2	16.8	29	28.6	15	10	17.8	
8.2	6.2	1.7	5.8	7	22.4	17	30	29.3	15.9	10	18.1	
8.2	6.3	1.8	6	7	24	17.9	30.2	30.5	16	10	18.7	
8.2	6.5	2	6.4	7.1	24.4	18.4	31.8	30.9	17.1	10.3	20.4	
8.5	6.6	2.1	6.5	7.1	24.7	18.6	34.4	31	17.7	10.6	20.4	
8.5	6.7	2.2	6.5	7.2	25	19	34.6	31.2	17.9	10.6	20.4	
8.9	7	2.7	6.7	7.4	25.2	19.7	35.4	32.1	18	10.7	20.5	
8.9	7.5	3	6.8	7.5	25.5	19.8	35.8	33.7	18.2	10.7	21.2	
9	7.6	3.1	7	7.5	25.9	19.8	38.5	34.4	18.4	10.7	21.3	
9.5	7.8	3.1	7	7.6	26	20.1	39.2	34.9	19.1	10.8	21.4	
9.8	7.9	3.2	7.2	7.7	27.8	21	39.8			10.9	16	
9.9	7	3.2	7.2	7.8	28	21.3	40.4			11	16.6	
9.9	6.7	3.2	7.3	7.9	28.1	21.3	45.4			11	17.2	
9.9		3.4	7.4	7.9	28.2	21.4				11	17.8	
10		3.4	7.5	8	28.3	21.4				11	18.2	
10.1		3.5	7.5	8.3	28.7	21.5				11.9	19	
10.1		3.6	7.5	8.5	29.8	21.6				12	19	
10.3		3.6	7.6	8.5	31.1	22.3				12.1	19.8	
10.3		3.7	8.1	8.7	32.5	22.3				12.3	19.9	
10.3		3.7	8.2	8.9	33.4	22.9				12.4	20.2	
10.4		3.8	8.2	9.1	34.1	23				12.4	21.2	
10.5		3.8	8.3	9.1	34.2	26.4				14	21.4	
10.5		3.8	8.7	9.3	35.2	14.2						
10.6		3.9	8.9	9.3	35.6	15.5						
10.9		3.9		9.6	37.8	18.7						
11		4		9.6		19.2						
11.1		4		10		19.3						
11.1		4		10.1		19.4						
11.1		4.1		10.6		19.5						
11.3		4.1				19.7						
11.3		4.1				20.5						
11.4		4.2				21						
11.4		4.2				21						
11.6		4.2				21						
12.1		4.3				21.2						
12.3		4.4				21.5						
12.5		4.4				21.8						
12.7		4.4				21.9						
12.7		4.4				22.3						
12.8		4.5				22.4						
12.9		4.5				22.6						
13		4.6				23.1						
13		4.6				23.3						
13.2		4.6				23.6						
13.5		4.6				24.1						
14.6		4.7				26.5						
15.9		4.7										
		4.8										

Devonian Brachiopods: Bulk Samples (length in mm)				Mississippian Brachiopods: Bulk Samples (length in mm)								
Li & Jones, 2003	Balinski, 1995			Balinski, 1997	Gordon et al., 1993							
<i>Nucleospira jens</i>	<i>Biernatella ovalis</i>	<i>Biernatella ventiformis</i>	<i>Biernatella polonica</i>	<i>Waiotrypa sulcicarina</i>	<i>Inflatia inflata</i>	<i>Inflatia cherokeensis</i>	<i>Inflatia cooperi</i>	<i>Inflatia clydensis</i>	<i>Inflatia gracilis</i>	<i>Inflatia pusilla</i>	<i>Adairia adairensis</i>	
		4.8										
		4.8										
		4.8										
		4.9										
		4.9										
		4.9										
		4.9										
		4.9										
		5										
		5.1										
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		8.3										

Ordovician-Devonian Bivalves: Bulk Samples (length in mm)						
Soot-Ryen, 1964		Sanchez et al., 1995		Babin & Melou, 1972	Sanchez, 1986	Sanchez, 1990
<i>Similodonta djupvikensis</i>		<i>Gotodonta gotlandica</i>		<i>Nuculites argentinum</i>		<i>Myoplusia contrastans</i>
					<i>Cadomia tya</i>	<i>Modiolopsis cuyana</i>
4	4.8	12		5.9		7
						16
4	5.3	12.1		6.5		8.5
						19
4.8	5.9	12.1		7.4		8.5
						19
4.9	6	12.2		7.7		9
						20
5.9	6.8	12.2		9		9.5
						21
6.2	7	13		9.4		10
						10
6.7	7	13.1		11		10.5
						22
6.9	7.5	13.2		11.6		10.5
						22
7.2	7.8	13.9		11.7		11
						11.5
7.3	8	14.9		12.5		12
						12
7.5	8	15.9		15		14
						15.5
8.1	8.2	16.7		17		16
						17
8.5	8.3	17.2		18		20
						22.4
8.9	8.7	17.9		18.6		25
						25
10.6	8.7	18		20		28
						28
	8.8	19.9		22.4		30
						30
	8.8	21.2		25		36
						36
	8.8	22.3		25		
	8.9	24		28		
	9	24.2				
	9.1	24.8				
	9.2	25.7				
	9.2					
	9.3					
	9.4					
	9.4					
	9.4					
	9.7					
	9.8					
	9.9					
	10					
	10.2					
	10.2					
	10.2					
	10.4					
	10.9					
	11.2					
	11.7					
	11.8					
	12					

Ordovician-Devonian Bivalves: Bulk Samples (length in mm)																	
Liljedahl, 1983						Liljedahl, 1984			Johnston, 1993								
<i>Nuculoidea lens</i>			<i>Nuculodonta gotlandica</i>			<i>Janeia silurica</i>	<i>Freja fecunda</i>		<i>Mytilarca bloomfeldensis</i>	<i>Cornelites catellus</i>	<i>Tolmala erugisulca</i>	<i>Goniophora duplisulca</i>	<i>Cypricardinia minima</i>	<i>Eoschizodus taemasensis</i>	<i>Crassatellopsis lenticularis</i>		
2.8	7.5	11.2	1.7	6.5	10.3	11.7	3.5	0.9	9.1	8	10	12	5	1.6	12.5	6.5	
2.8	7.5	11.2	1.7	6.5	10.3	11.7	5.25	1	9.2	13	12	15.5	5.25	1.9	12.5	6.75	
3.1	7.7	11.2	2.2	6.5	10.3	11.7	6.75	1.3	10.2	15.5	13.5	20	8	2	15	8	
3.1	7.7	11.3	2.2	6.5	10.3	11.7	6.75	1.3	11.1	16	14.5	22	10	2.1	17.5	8.25	
3.3	7.9	11.3	2.3	6.7	10.4	11.8	7.5	1.7	11.8	17.5	16.5	23.5	10	2.4	18.5	9.5	
3.4	9	11.3	2.3	6.7	10.5	11.9	11.75	1.7	11.8	19	18	24	11	2.6	18.5	9.5	
3.5	9	11.3	2.5	6.8	10.6	11.9	12.75	2	11.9	20	22	29.5	12	2.7	19	11	
3.5	9	11.5	2.5	6.8	10.6	11.9	15	2	12.3	20.5	22	30	12	2.9	20	11	
3.5	9	11.5	2.7	7.4	10.6	11.9	15.1	2.3	12.7	25	24	41.5	12.5	3	22	11.5	
3.5	9.1	11.6	2.7	7.6	10.6	11.9	16.25	2.3	12.8	26	25	41.5	14	3.2	22.5	11.75	
3.6	9.3	11.6	3.6	7.6	10.8	11.9	17.5	2.8	12.9	27	28	46	14.5	3.75	23	12.25	
3.8	9.3	11.6	3.6	7.7	10.8	11.9	17.5	2.8	12.9	32	38.5	50	15.5	3.8	24	14	
3.8	9.4	11.7	3.6	7.8	10.8	12	17.9	2.8	13.2	32	40.5	57	17.25	3.8	26	14.5	
3.9	9.4	11.8	3.8	8.1	10.8	12.1	18.1	3.1	13.7		46	58	17.5	4.8	26.5	16	
4	9.5	11.8	3.8	8.3	10.8	12.1	19.9	3.2	14.6			66	18	5.1		17	
4	9.6	11.9	4	8.4	10.9	12.2	20.1	3.2				70	18.5	5.2			
4.1	9.6	12	4.2	8.5	10.9	12.3	23	3.2					19	5.2			
4.1	9.7	12	4.2	8.7	10.9	12.3	28.75	3.3					19	5.6			
4.2	9.7	12.1	4.3	8.8	10.9	12.3		3.5					19.25				
4.2	9.8	12.1	4.3	8.8	10.9	12.4		3.7					19.5				
4.5	9.8	12.1	4.3	8.9	11	12.5		4					20				
4.5	9.8	12.1	4.4	8.9	11	12.5		4.1					20.25				
4.8	9.9	12.2	4.4	8.9	11	12.5		4.4					20.75				
4.8	10	12.2	4.5	9	11.1	12.6		4.6					21				
4.9	10	12.2	4.5	9.1	11.1	12.8		4.6					22.5				
4.9	10	12.3	4.6	9.1	11.2	12.9		4.7					26				
5	10.1	12.3	4.6	9.3	11.3	12.9		4.8									
5	10.1	12.5	4.7	9.3	11.3	12.9		5									
5.2	10.1	12.5	4.7	9.3	11.3	13		5.2									
5.3	10.1	12.6	5	9.4	11.3	13.1		5.3									
5.6	10.2	12.8	5	9.4	11.3	13.1		5.5									
5.6	10.3	12.8	5	9.4	11.3	13.2		5.6									
5.8	10.3	12.8	5	9.6	11.4	13.2		5.8									
5.8	10.3	12.8	5.1	9.6	11.4	13.2		6.5									
5.8	10.3	13.2	5.4	9.6	11.4	13.5		6.5									
5.8	10.3	13.5	5.4	9.7	11.5	13.5		6.7									
6	10.3	14.4	5.5	9.7	11.5	13.7		6.8									
6	10.6	14.4	5.5	9.7	11.5	13.8		7									
6.2	10.7	14.4	5.5	9.7	11.5	13.8		7.2									
6.2	10.7	14.4	5.5	9.8	11.6	14		7.3									
6.5	10.7	14.6	5.6	9.8	11.6	14.1		7.4									
6.7	10.9	14.7	5.7	9.9	11.7	14.2		7.8									
6.7	10.9	14.8	5.7	10	11.7	14.4		8									
6.8	10.9	15	5.8	10	11.7	14.5		8.2									
7	10.9		5.9	10	11.7	14.6		8.4									
7.1	11		5.9	10	11.7	14.7		8.4									
7.3	11		6	10	11.7	14.7		8.9									
7.4	11		6	10.1	11.7	14.7		9									
7.4	11.1		6.5	10.1	11.7	15.3		9									
					15.3	9											

Miocene-Pliocene Bivalves: Bulk Samples (length in mm)																	
Bird, 1965			Amano, 1986	Lauriat-Rage, 1982													
<i>Anadara transversa 1</i>	<i>Anadara transversa 2</i>	<i>Anadara transversa 3</i>	<i>Glycymeris idensis</i>	<i>Astarte omalii omalii</i>	<i>Astarte omalii scalaris 1</i>			<i>Astarte omalii scalaris 2</i>			<i>Astarte soliculula</i>	<i>Digitaria digitaria 1</i>		<i>Digitaria digitaria 2</i>	<i>Astarte fusca incrustata</i>		
10	27.8	15.2	28.6	10.75	8.75	13	16.8	13	6.25	14.4	17.1	5.45	8.38	4.68	6.03	5.1	7.5
10.3	28.9	18.4	29.3	11.6	8.75	13.25	16.8	13	7.6	14.5	17.25	5.67	8.39	4.82	5.99	5.39	9.5
10.6	30.5	19.1	29.4	18.2	8.75	13.3	16.9	16.7	7.9	14.5	17.5	5.97	8.51	4.89	6	5.48	10.5
11.3	31.2	24.6	33.8	19.8	9.25	13.3	16.9	16.8	8.9	14.5	17.75	5.87	8.51	4.9	5.97	5.51	10.5
12.9	31.3	26.4	30.5	21.6	9.25	13.4	16.9	22.3	10.25	14.5	17.75	6	8.83	4.86	6.1	5.61	11.5
13	32.1	28.6	36.8	22.4	9.5	13.4	17	20.6	10.3	14.7	17.9	6.06	8.68	5.12	6.17	5.61	11.5
13.5	33	29.4	32.6	22.5	9.5	13.6	17	20.7	10.3	14.7	17.9	6.11	8.7	5.16	5.94	5.66	12.5
14	33.6	29.5	31.8	23.5	9.75	13.6	17	21.1	10.6	14.9	18	6.09	8.57	4.93	6.05	5.66	12.5
14.4	33.8	36.6	28.3	23.6	9.75	13.75	17		10.75	14.9	18.4	6.19	8.7	5.35	6.4	5.68	12.5
14.6	34.5	37.4	33.8	23.6	10	13.8	17.25		11.1	14.9	18.7	6.19	8.69	5.42	5.89	5.69	12.5
14.6	35.5	40.7	36.4	23.6	10	13.9	17.25		11.25	14.9	14.4	6.25	8.77	5.33	5.99	5.7	13.5
14.6	35.5	42.7	35.2	23.8	10	14.2	17.4		11.3	15	14.4	6.43	9.03	5.3	6.05	5.72	13.5
14.7	36.1	44.8	33.4	24.5	10.25	14.5	17.4		11.6	15.1	14.4	6.37	9.08	5.46		5.75	13.5
15	36.6	45	33.3	24.9	10.25	14.5	17.4		11.6	15.25	17	6.31	9.2	5.33		5.77	13.5
15.1	37.7	47.4	30	25.1	10.25	14.6	17.4		11.8	15.25	17.1	6.39	9.31	5.42		5.78	13.5
15.2	38.1	49.1	34.4	27.4	10.25	14.6	17.5		11.9	15.25	17.1	6.52	9.35	5.52		5.78	13.5
15.4	38.4	50.1	29.4	28	10.25	14.7	17.5		11.9	15.4		6.61	9.59	5.64		5.78	13.5
15.5	40.7	52.7	38	28	10.5	14.8	17.6		12	15.5		6.79	9.73	5.17		5.8	14.5
15.5	41.3	53.6	27.4	28.5	10.5	14.9	17.6		12	15.6		6.55	9.8	5.24		5.8	14.5
15.6	42.6	54	26.1	29.4	10.5	14.9	17.7		12.1	15.6		6.36	9.87	5.33		5.84	14.5
16			31	30.4	10.75	14.9	17.7		12.25	15.6		6.32	9.91	5.33		5.85	14.5
16			29.4	30.5	10.75	14.9	17.75		12.4	15.6		6.49	10	5.36		5.86	14.5
16.2			28.8	31.5	10.8	15	17.75		12.4	15.7		6.46	10	5.37		5.9	14.5
16.3			28.1	32.4	10.8	15	17.75		12.6	15.7		6.76	10	5.4		5.91	14.5
16.3			29.5	33.3	10.8	15	17.75		12.6	15.8		6.7	10	5.46		5.92	14.5
16.5			36.4	33.75	11	15	17.75		12.7	15.8		6.65	10.2	5.49		5.93	14.5
16.6			34.7	36.5	11	15	17.75		12.75	15.8		6.86	10.3	5.46		5.96	14.5
17.2			25	36.6	11	15.1	17.75		12.75	15.8		6.94	10.4	5.51		5.97	14.5
17.4			34	36.9	11.1	15.3	17.9		12.8	15.8		6.91	10.5	5.56		5.98	14.5
17.5			29.4		11.1	15.5	17.9		12.8	15.9		6.87	10.5	5.52		5.99	14.5
18			28.9		11.25	15.5	17.9		13	15.9		6.88	10.7	5.59		6	14.5
18.1			31.3		11.5	15.9	18		13	16		7.03	10.8	5.58		6.04	14.5
18.2			32.5		11.5	15.9	18.2		13	16		7.05	10.8	5.55		6.07	15.5
18.2			30.3		11.75	15.9	18.2		13	16		7.18	11	5.6		6.09	15.5
18.2			26		11.75	15.9	18.2		13.2	16.1		7.4	11.2	5.59		6.11	15.5
18.3			30		11.8	16	18.25		13.25	16.1		7.79	11.3	5.68		6.15	15.5
18.9			35.7		11.8	16	18.25		13.25	16.2		7.03	11.4	5.68		6.19	15.5
19.1			35		11.9	16	18.4		13.4	16.2		7.1	12	5.62		6.24	15.5
19.1			34.3		11.9	16	18.6		13.4	16.2		7.29	13.3	5.7			15.5
19.5			31		11.9	16	18.75		13.4	16.4		7.74	12.5	5.64			15.5
19.5			33.5		11.9	16	18.9		13.4	16.4		7.35	13.3	5.71			15.5
20			32.7		12	16	19		13.5	16.4		7.2	8.11	5.63			15.5
20			33.1		12	16.1	19		13.5	16.4		7.19	8.2	5.61			15.5
20			32		12.25	16.1	19.4		13.6	16.5		7.27	8.32	5.63			15.5
20			35.8		12.25	16.1	19.4		13.6	16.5		7.52		5.66			16.5
20.3			34		12.3	16.2	19.5		13.75	16.5		7.51		5.74			16.5
20.4			32		12.3	16.2	19.5		13.75	16.5		8.05		5.74			16.5
20.5			27.5		12.3	16.3	19.6		13.8	16.5		7.95		5.81			16.5
20.9			29.8		12.5	16.3	19.8		13.9	16.7		7.58		5.89			16.5
21			30.4		12.5	16.3	19.8		13.9	16.7		7.64		5.86			17.5
22					12.6	16.5	19.8		14	16.7		7.82		5.81			
22					12.7	16.5	20		14	16.75		7.74		5.66			
22.3					12.75	16.6	20		14	16.9		7.84		5.82			
22.5					12.9	16.6	20.25		14	16.9		8.34		5.92			
					13	16.6	20.25		14.2	16.9		8.13		5.93			
					13	16.7	20.25		14.2	17		8.05		5.89			

Miocene-Pliocene Bivalves: Bulk Samples (length in mm)

Lauriat-Rage, 1982		Jung, 1996									
<i>Astarte sulcata redonensis</i> 1	<i>Astarte sulcata redonensis</i> 2	<i>Cardiomya (Cardiomya) isahispaniolae</i>	<i>Cardiomya (Bowdenia) distira</i>	<i>Plectodon granulatus</i>	<i>Haliris hamaicensis</i>	<i>Trigonulina ornata</i>	<i>Trigonulina pacifica</i>	<i>Trigonulina pacifica</i>	<i>Trigonulina pacifica</i>	<i>Trigonulina pacifica</i>	<i>Trigonulina bowdenensis</i>
8.5	8.5	4.77	2.5	8.4	2.96	2.3	3.78	1.8	3.8	4.9	1.49
10.5	9.5	4.69	2.39	8.5	3.17	2.4	3.78	1.9	3.69	4.8	1.69
12.5	9.5	4.99	2.59	8.6	3.17	2.59	3.88	1.9	3.6	4.69	1.79
12.5	9.5	4.88	2.49	9.2	3.28	2.7	3.99	2	3.49	4.6	1.89
12.5	10.5	5.28	2.59	8.8	3.48	2.8	4.09	2.21	4.19	4.49	1.99
12.5	10.5	5.29	2.49	9.61	3.88	2.8	4.19	2.11	4.09	4.39	2.09
12.5	10.5	5.28	2.9	9.9	3.78	2.7	4.39	2.3	3.99	4.29	1.89
13.5	11.5	5.58	2.8	9.91	4.28	2.79	4.29	2.4	3.8	4.39	1.99
13.5	11.5	7.29	2.8	10.4	4.28	2.79	4.19	2.3	3.69	4.49	2.08
13.5	11.5	6.29	2.8	10.6	4.48	2.89	3.99	2.7	3.69	4.59	2.19
13.5	11.5	5.39	2.89	11.5		2.89	3.99	2.79	3.79	4.7	2.29
13.5	11.5	6.4	2.89	11.5		3.1	4.19	2.7	3.9	4.8	2.19
13.5	11.5	5.89	2.99	11.3		2.99	4.19	2.6	4.08	4.9	2.08
13.5	11.5	7.49	2.99	12.2		2.99	4.58	2.51	4.19	4.9	1.99
13.5	11.5	7.69	2.99	12		3.09	4.8	2.41	4.49	4.8	1.98
13.5	11.5	7.6	2.89	11.7		3.09	4.49	2.6	4.39	4.69	2.08
13.5	11.5	6.99	3.2	11.9		3.19	4.4	2.7	3.99	4.59	2.19
14.5	12.5	7.39	3.09	13.3		3.19	5	2.8	3.89	4.49	2.29
14.5	12.5	8.4	3.2	14.4		3.29		2.79	3.79	4.59	2.29
14.5	12.5	7.99	3.09	13.3		3.29		2.6	3.69	4.69	2.19
14.5	12.5	9.3	3.2			3.19		2.6	3.78	4.8	2.08
14.5	12.5	8.2	3.29			3.2		2.8	3.89	4.9	1.98
14.5	12.5	8.4	3.29			3.29		2.89	3.99	5	2.29
14.5	12.5	8.72	3.19			3.39		3.2	4.08	5.1	2.38
14.5	12.5	9.1	3.29			3.5		2.99	4.18	5	2.49
15.5	12.5		3.39			3.59		2.89	4.29	4.89	2.39
15.5	12.5		3.7			3.78		2.79	4.4	4.79	2.59
15.5	12.5		3.3			3.78		2.79	4.49	4.69	2.69
15.5	13.5					3.59		2.89	4.39	4.79	2.69
15.5	13.5					3.49		3	4.29	4.9	2.59
15.5	13.5					3.39		3.09	4.18	5	2.59
15.5	13.5					3.29		3.19	4.08	5.1	2.69
15.5	13.5					3.29		2.99	3.99	5	2.89
16.5	13.5					3.39		3.19	3.89	4.89	3
16.5	13.5					3.49		3.29	3.99	5	2.78
16.5	13.5					3.59		3.09	4.08	5.09	2.68
16.5	13.5					3.68		3.19	4.18	5	2.68
16.5	13.5					3.78		3.4	4.29	5.1	2.78
16.5	13.5					3.89		3.29	4.39	5.2	3
16.5	13.5					3.79		3.39	4.49	5.3	3.08
16.5	13.5					3.68		3.49	4.69	5.8	2.88
17.5	14.5					3.58		3.59	4.59	5.2	2.78
17.5	14.5					3.39		3.8	4.49	5.4	3.08
17.5	14.5					3.68		4	4.39		3.38
17.5	14.5					3.78		3.89	4.28		2.99
17.5	15.5					3.89		3.49	4.19		3.29
17.5	15.5					3.99		3.39	4.09		3.48
17.5	15.5					4.09		3.3	3.99		3.59
17.5	15.5					3.99		3.19	4.19		3.8
17.5	15.5					3.88		3.39	4.29		3.99
	17.5					3.78		3.49	4.39		3.79
						3.68		3.59	4.5		3.69
						3.58		3.69	4.59		3.79
						4.09		3.79	4.69		3.89
						3.99		3.99	4.8		
						3.88		3.89	5.01		

Appendix 2.2: Monograph raw data

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Ordovician Brachiopods							
Alberstadt, 1979							
<i>Platystrophia annieana</i>	Plate 4:1	1.1	26.6	24.2	39.6	36.0	100
USGS collection 7834-CO	Plate 4:3	1.1	22.5	20.5	32.6	29.6	100
	Plate 4:4	1.1	24.4	22.2	40.5	36.8	100
	Plate 4:5	1.1	21.4	19.5	30.0	27.3	96.5
<i>Platystrophia colbienesis</i>	Plate 5:31	1.2	16.0	13.3	21.6	18.0	78.5
USGS collection 7812-CO	Plate 5:32	1.2	19.8	16.5	27.6	23.0	100
	Plate 5:33	1.2	16.4	13.7	22.1	18.4	85
	Plate 5:34	1.2	14.1	11.8	19.3	16.1	71.5
<i>Platystrophia elegantula</i>	Plate 5:70	1.2	12.5	10.4	17.1	14.3	10
USGS collection 4982-CO							
<i>Platystrophia ponderosa</i>	Plate 2:22	1.1	30.9	28.1	40.6	36.9	64.5
USGS collection 4556-CO	Plate 2:23	1.1	27.6	25.1			38.5
	Plate 2:24	1.1	21.7	19.7	29.3	26.6	3
	Plate 2:25	1.1	26.9	24.5			32.5
	Plate 2:26	1.1	26.4	24.0	34.5	31.4	32
	Plate 4:22	1.1	21.5	19.5	26.7	24.3	8
	Plate 4:23	1.1	13.6	12.4	17.4	15.8	1
Howe, 1979							
<i>Sowerbyella sp.</i>	Plate 2:5	3	20.0	6.7	39.3	13.1	60.5
USGS collection 8068-CO	Plate 2:6	3	22.7	7.6	43.4	14.5	79
	Plate 2:7	3	21.6	7.2	42.6	14.2	72
	Plate 2:11	3	34.0	11.3	72.2	24.1	100
	Plate 2:13	5	44.2	8.8	82.1	16.4	100
<i>Rhyncotrema increbescens</i>	Plate 3:1	2.5	22.8	9.1	24.3	9.7	31.5
USGS collection 5015-CO	Plate 3:7	2.5	25.2	10.1	26.6	10.6	58.5
	Plate 3:13	2.3	29.0	12.9	29.8	13.2	95
	Plate 3:18	2.3	29.1	12.9	33.8	15.0	96.5
	Plate 3:19	2.3	29.9	13.3	33.9	15.1	100
	Plate 3:22	3	33.4	11.1	32.0	10.7	65.5
	Plate 3:23	3	38.3	12.8	38.8	12.9	94
<i>Orthorhynchula linneyi</i>	Plate 4:13	1.5	20.4	13.6	22.3	14.9	45
USGS collection 6409-CO	Plate 4:16	1.5	34.1	22.7	38.5	25.7	100
	Plate 6:1	3	52.0	17.3	56.3	18.8	73

FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)	
Howe, 1979							
<i>Orthorhynchula sublinneyi</i>	Plate 4:21	1.5	23.9	15.9	25.7	17.1	26
USGS collection 5036-CO	Plate 4:24	1.5	33.8	22.5	33.9	22.6	100
USGS collection 5095-CO	Plate 4:28	1.5	34.1	22.7	42.9	28.6	100
	Plate 4:31	1.5	30.7	20.5	39.3	26.2	92.5
	Plate 5:11	3	43.3	14.4	60.3	20.1	16
	Plate 5:12	3	40.8	13.6	50.9	17.0	12.5
	Plate 5:15	3	55.8	18.6	69.3	23.1	81
Pope, 1979							
<i>Oepikina minnesotensis</i>	Plate 1:2b	2	32.2	16.1	35.7	17.9	75.5
USGS collection 5078-CO	Plate 1:6b	2	34.6	17.3	39.6	19.8	91.5
	Plate 1:7b	2	31.1	15.6	35.9	18.0	72.5
	Plate 1:8b	2	32.8	16.4	36.4	18.2	77
	Plate 1:9b	2	30.9	15.5	38.5	19.3	72.5
	Plate 1:10	2	31.2	15.6	37.2	18.6	73
	Plate 1:11b	2	27.5	13.8	30.5	15.3	40.5
	Plate 1:12b	2	27.2	13.6	32.3	16.2	40
	Plate 1:13	1	17.5	17.5	20.4	20.4	95
	Plate 1:14b	2	23.8	11.9	27.5	13.8	21
	Plate 2:1b	2	37.3	18.7	41.1	20.6	100
	Plate 2:2b	2	30.2	15.1	35.2	17.6	65
	Plate 2:3b	2	37.7	18.9	42.3	21.2	100
	Plate 2:4a	2	36.7	18.4	40.8	20.4	100
	Plate 2:7b	2	22.9	11.5	26.7	13.4	13.5
	Plate 2:8b	2	22.9	11.5	29.1	14.6	13.5
	Plate 2:9b	2	33.4	16.7	37.4	18.7	82
	Plate 3:9a	2	25.6	12.8	34.3	17.2	33
	Plate 3:10	2	25.2	12.6	30.9	15.5	28
	Plate 3:11	2	28.6	14.3	35.2	17.6	52
	Plate 3:13a	2	27.1	13.6	31.4	15.7	39.5
	Plate 3:14	2	24.6	12.3	28.7	14.4	25.5
	Plate 3:15	2	26.1	13.1	30.3	15.2	35
	Plate 3:17	2	30.1	15.1	34.3	17.2	64.5
	Plate 3:18	2	30.0	15.0	34.9	17.5	64.5
	Plate 3:19	2	29.1	14.6	35.9	18.0	57.5

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
<i>Oepikina minnesotensis</i>	Plate 1:1b	2	31.7	15.85	36.5	18.25	87
USGS collection 7875-CO	Plate 1:3b	2	33.1	16.55	32.8	16.4	92.5
	Plate 1:4b	2	32.7	16.35	33.9	16.95	91
	Plate 1:5b	2	31.3	15.65	32.8	16.4	86
	Plate 2:5	2	30.8	15.4	38.9	19.45	81
	Plate 2:6	2	35.9	17.95	32.2	16.1	98.5
	Plate 3:1	2	30.3	15.15	35	17.5	78
	Plate 3:2	2	32.5	16.25			90.5
	Plate 3:3	2	30.3	15.15	37.7	18.85	78
	Plate 3:4	2	26.4	13.2	31.2	15.6	9.5
	Plate 3:5	2	30.1	15.05	35.6	17.8	77.5
	Plate 3:7	2	25.3	12.65	33.4	16.7	6
	Plate 3:8	2	29.6	14.8	35.7	17.85	65
<i>Pionomena recens</i>	Plate 7:16	2.5	29.2	11.68	39.7	15.88	100
USGS collection 5015-CO	Plate 7:18	2.5	17.9	7.16	20.4	8.16	63.5
	Plate 7:21a	2.5	18.2	7.28	23.5	9.4	64.5
	Plate 7:22a	2.5	20.5	8.2	27	10.8	84
	Plate 7:23	2.5	21.1	8.44	27.7	11.08	87.5
	Plate 7:24	2.5	25.5	10.2	34.6	13.84	98
	Plate 7:25	2.5	23.7	9.48	30.4	12.16	96
	Plate 7:26	2.5	18.5	7.4	25.8	10.32	68
	Plate 7:27	2.5	21.5	8.6	29.9	11.96	89
	Plate 7:20a	2.5	19	7.6	26.1	10.44	72
Silurian Brachiopods							
Amsden, 1968							
<i>Dicoelosia bilobella</i>	Fig. 3.6a USNM 158103	5	16.04	3.208			96
St. Clair Limestone, Arkansas	Fig. 3.6f USNM 158104	5	15.97	3.194			90
	Fig. 8.2a USNM 158105	5	9.84	1.968			12
	Fig. 8.2c USNM 158106	5	15.21	3.042			84
	Fig. 8.2e USNM 158107	5	16.9	3.38			96
<i>Dicoelosia oklahomensis</i>	Fig. 8.4a OU6283	5	15.01	3.002			61
Henryhouse Fm., Oklahoma	Fig. 8.4c OU6284	5	16.56	3.312			84
	Fig. 8.4d OU6285	5	15.57	3.114			76

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
<i>Antirhynchonella thomasi</i>	Fig. 4.1d USNM 158137	2	16.47	8.235			17
St. Clair Limestone, Arkansas	Fig. 4.1e USNM 158138	2	20.34	10.17			55
	Fig. 4.1i OU 6266	2	18.73	9.365			34
	Fig. 4.1k OU 6267	1	14.37	14.37			100
	Fig. 4.1l OU 6268	1	13.59	13.59			100
	Fig. 4.1r USNM 158139	2	20.95	10.475			62
	Fig. 4.1o USNM 158140	2	19	9.5			36
	Fig. 4.1s USNM 158143	2	17	8.5			23
	Fig. 4.1t USNM 158144	2	17.98	8.99			28
<i>Hircinisca havliceki</i>	Fig. 5.5e USNM 158206	2	15.85	7.925			100
St. Clair Limestone, Arkansas	Fig. 5.5f USNM 158207	3	22.66	7.5533			82
	Fig. 5.5k USNM 158208	3	23.29	7.7633			91
	Fig. 5.5n USNM 158209	3	17.11	5.7033			9
<i>Eospirifer acutolineatus acutolineatus</i>	Fig. 1.1b USNM 158045	1	17.31	17.31			86
St. Clair Limestone, Arkansas	Fig. 1.1f USNM 158047	1	12.44	12.44			73
	Fig. 1.1i USNM 158049	1	21.07	21.07			100
	Fig. 1.1l USNM 185050	2	20.79	10.395			42
	Fig. 1.1s USNM 158051	2	19.81	9.905			37
<i>Eospirifer acutolineatus pentagonus</i>	Fig. 2.2a USNM 158059	1	17.97	17.97			74
St. Clair Limestone, Arkansas	Fig. 2.2d USNM 158060	1	19.43	19.43			87
	Fig. 2.2e USNM 158061	1	18.06	18.06			74
	Fig. 2.2j USNM 158062	1	18.09	18.09			74
	Fig. 2.2k USNM 158063	1	19.58	19.58			87
	Fig. 2.2q USNM 158065	1	14.17	14.17			53.5
<i>Kozlowskiellina (K.) vaningeni</i>	Fig. 2.1a USNM 158070	3	18.4	6.1333			9
St. Clair Limestone, Arkansas	Fig. 2.1e USNM 158071	3	20.01	6.67			20
	Fig. 2.1f USNM 158072	3	21.55	7.1833			39
	Fig. 2.1l USNM 158073	3	14.9	4.9667			2.5
	Fig. 2.1q USNM 158075	1	11.69	11.69			93.5
	Fig. 2.1s USNM 158076	2	20.87	10.435			80.5
<i>Atrypina erugata</i>	Fig. 10.4b USNM 158227	3	16.53	5.51			84.5
St. Clair Limestone, Arkansas	Fig. 10.4d USNM 158229	3	16.51	5.5033			84.5
	Fig. 10.4o USNM 158231	4	21.29	5.3225			78.5
	Fig. 10.4h USNM 158232	3	18.92	6.3067			94.5
	Fig. 10.4n USNM 158233	3	24.95	8.3167			100

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
<i>Nanospira clarensis</i>	Fig. 6.2c USNM 158124	3	15.41	5.1367			65.5
St. Clair Limestone, Arkansas	Fig. 6.2i OU 6264	3	16.28	5.4267			67.5
	Fig. 6.2j USNM 158125	3	15.65	5.2167			65.5
	Fig. 6.2l USNM 158126	3	22.32	7.44			92.5
	Fig. 6.2m YPM 25727	3	26.13	8.71			97
	Fig. 6.2s OU 6265	3	18.9	6.3			79
	Fig. 6.2t USNM 158129	3	22.42	7.4733			92.5
	Fig. 6.2v USNM 158130	3	22.1	7.3667			89
	Fig. 6.2w USNM 158131	3	29.59	9.8633			100
	Fig. 6.2y USNM 158132	3	21.87	7.29			87
	Fig. 6.2zz USNM 158133	3	22.4	7.4667			92.5
<i>Dicamaropsis parva</i>	Fig. 9.1b USNM 158748	2	18.58	9.29			89
St. Clair Limestone, Arkansas	Fig. 9.1e USNM 158749	2	21.52	10.76			100
	Fig. 9.1h USNM 158750	2	20.36	10.18			96.5
	Fig. 9.1m USNM 158751	2	18.02	9.01			86
	Fig. 9.1q USNM 158752	2	15.68	7.84			75.5
	Fig. 9.1t OU6419	3	20.69	6.8967			64
	Fig. 9.1u USNM 158753	2	19.26	9.63			94
	Fig. 9.1v USNM 158754	2	18.88	9.44			91.5
	Fig. 9.1x USNM 158755	2	17.67	8.835			84.5
	Fig. 9.1y OU 6420	2	16.23	8.115			80
	Fig. 9.3b YPM 25745	3	15.22	5.0733			26
	Fig. 9.5b YPM 25747	3	15.28	5.0933			26
	Fig. 9.6a YPM 25748	3	18.84	6.28			56
<i>Meristina clarensis</i>	Fig. 10.2b USNM 158222	1	14.95	14.95			90.5
St. Clair Limestone, Arkansas	Fig. 10.2e USNM 158224	1	18.59	18.59			100
	Fig. 10.2i USNM 158225	1	15.18	15.18			90.5
Devonian Brachiopods							
Li & Jones, 2003							
<i>Nucleospira lens</i>	Fig 13.8 UA 12961	4	38.23	9.5575	40.17	10.043	24
81C-186m							
Baad Fiord							
Grinnell Peninsula							
Balinski, 1995							
<i>Biernatella ovalis</i>	ZPAL BP XXXVIII/25-8			6.7		6.7	59
	ZPAL BP XXXVIII/25-10			7.7		6.7	86.5
	ZPAL BP XXXVIII/25-5			7.6		7.3	86
	ZPAL BP XXXVIII/25-9			7.9		6.8	100

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
<i>Biernatella lentiformis</i>	ZPAL BP XXXVIII/32-76			5.8		5.7	73
	ZPAL BP XXXVIII/32-22			4.1		3.3	32
	ZPAL BP XXXVIII/32-85			6.5		6.2	84
	ZPAL BP XXXVIII/32-75			5.9		5.6	74
	ZPAL BP XXXVIII/32-97			8.4		8.8	100
	ZPAL BP XXXVIII/83			6.4		5.7	82.5
	ZPAL BP XXXVIII/32-81			6.2		6.2	80
<i>Biernatella polonica</i>	ZPAL BP XXIII/30g			7		6.8	46
Balinski, 1997							
<i>Waiotrypa sulcicarina</i>	GIUS 284/117	2	18.5	9.25	22.55	11.275	78
	GIUS 284/122	2	19.79	9.895	24.25	12.125	91
	GIUS 284/121	2	18.69	9.345	24.24	12.12	83
Mississippian Brachiopods							
Gordon et al., 1993							
<i>Inflatia inflata</i>	USNM 123977a			35.6			96
NMNH loc. 568	USNM 123977b			37.8			98
<i>Inflatia cherokeensis</i>	USNM 218947x			24.1			95
NMNH loc. 568 & 569	CAS 6603.01			23			86
<i>Inflatia cooperi</i>	USNM 218964			35.8			66
NMNH loc. 469	USNM 218968			31.8			39
<i>Inflatia clydensis</i>	USNM 218954			29.3			33
USGS coll. 7088	USNM 218955			32.1			74
<i>Inflatia gracilis</i>	USNM 218972			18			73
NMNH loc. 568							
<i>Inflatia pusilla</i>	USNM 218981			10.9			54
NMNH loc. 570							
<i>Adairia adairensis</i>	USNM 218966c			17.8			29
NMNH loc. 566 & 568	USNM 218966a			21.2			87

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Paleocene-Eocene Brachiopods							
Cooper, 1988							
<i>Plicatoria wilmingttonensis</i>	2.21.USNM550866	1	27.33	27.33			56
Wilmington, NC	2.28.USNM550870	1	32.36	32.36			74.5
USGS loc. 3602 (North Carolina 1)	7.4.USNM549389i	1	39.5	39.5			98
	7.5.USNM549389e	1	34.22	34.22			81.5
	7.11.USNM549389-1	1	33.94	33.94			81.5
	7.13.USNM549389c	1	33.95	33.95			81.5
	7.20.USNM549389f	1	33.77	33.77			81.5
	7.24.USNM549389d	1	36.86	36.86			90.5
	8.2.USNM549389h	1	37.81	37.81			92
	8.7.USNM550874	1	23.31	23.31			33
	8.9.USNM549389k	1	33.73	33.73			81.5
	9.9.USNM550877	1	15.48	15.48			6
	9.15.USNM550865a	1	38.98	38.98			97
	9.17.USNM550869	1	33.01	33.01			81
	9.21.USNM550873	1	27	27			52.5
	9.27.USNM551524	1	20.29	20.29			18
	9.28.USNM550812	1	39.99	39.99			98.5
	9.31.USNM548398n	1	25.77	25.77			44
	9.33.USNM550876	1	43.6	43.6			100
	9.34.USNM550867	1	25.39	25.39			43.5
	9.35.USNM550880	1	35.29	35.29			87
	9.39.USNM550811	1	15.88	15.88			8.5
	9.40.USNM550868	1	38.77	38.77			96
	9.2.USNM550879	1	21.9	21.9			27
	9.13.USNM550810a	1	13.61	13.61			4
<i>Plicatoria wilmingttonensis</i>	8.14.USNM551495a	1	31.37	31.37			84.5
Ideal Cement Company Quarry	8.17.USNM551499	1	23.78	23.78			37
Loc: North Carolina 2	8.21.USNM551502	1	30.81	30.81			81.5
	8.22.USNM551494a	1	33.16	33.16			89.5
	8.27.USNM551497a	1	32.45	32.45			87
	8.29.USNM551496a	1	40.06	40.06			99.5
	8.31.USNM551501	2	30.41	15.205			3
	8.32.USNM551500	2	44.69	22.345			23.5
<i>Terebratulina wilsoni</i>	1.15.USNM551515a	3	41.57	13.857			86
Loc.: South Carolina 4	6.29.USNM?	2	25.29	12.645			56.5
<i>Terebratulina lachryma</i>	1.16.USNM551516a	3	47.72	15.907			100
Loc.: South Carolina 2							

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Craig, 2000							
<i>Basiliola sp.</i>	1.10.WAM84.588c	3.8	27.53	7.3413			47
Upper Paleocene	1.12.WAM84.588a	4	35.16	8.79			86.5
	1.15.WAM84.584	4	30.73	7.6825			61
<i>Giraliathyris mcnamarai</i>	2.3.WAM96.826	3	71.22	23.74			41.5
Upper Paleocene							
<i>Giraliathyris kaitrinae</i>	3.2.WAM84.547	2	54.91	27.455			82
Upper Paleocene	3.4.WAM96.609	2.6	54.37	20.912			25.5
<i>Giraliathyris jubileensis</i>	2.6.WAM84603e	2	74.84	37.42			95
Middle Eocene	2.7.WAM84.604e	2	72.12	36.06			88.5
	3.1.WAM84.604i	2	54.81	27.405			31.5
<i>Victorithyris decapello</i>	3.9.WAM96.645	2	59.92	29.96			87.5
Upper Paleocene	4.2.WAM96.607	2	60	30			87.5
<i>Victorithyris blakeorum</i>	4.3.WAM96.706	2.5	54.64	21.856			94
Upper Paleocene	4.5.WAM96.697	2.5	52.12	20.848			92
	4.7.WAM88.111b	2.5	54.96	21.984			94
	4.9.WAM88.111a	2.5	61.01	24.404			100
Ordovician-Devonian Bivalves							
Soot-Ryen, 1964							
<i>Similodonta djupvikensis</i>	MO 21934			10.7			100
Middle Silurian							
<i>Gotodonta gotlandica</i>	MO 150371			23.5			94
Middle Silurian	MO 150774			23.2			94
	MO 150236			11.8			62
	MO 14988			8.6			21
Sanchez et al., 1995							
<i>Nuculites argentinum</i>	3.11.CORD-PZ8687	2	50.1	25.05			94
Late Silurian - Early Devonian	3.12.CEGH-UNC1449	2	37.99	18.995			73
	3.13.CORD-PZ8689	2.5	48.44	19.376			74
	3.15.CEGH-UNC1441	1.5	34.2	22.8			84
	3.16.CEGH-UNC1451	3	31.58	10.527			32
	3.17.CORD-PZ8901	5.5	38.21	6.9473			10.5
	3.19.CEGH-UNC1446	2	31.69	15.845			57.5

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Babin & Melou, 1972							
<i>Myoplusia contrastans</i>	VII.8.LPB1438	4	48.29	12.073			76
Ordovician, Caradoc	VII.9.LPB1436	4	44.3	11.075			58
	VIII.1.LPB1437	6	56.96	9.4933			24
	VIII.3.LPB1439	5.5	54.58	9.9236			30
Sanchez, 1996							
<i>Cadomia typa</i>	1.1.8046	2	36.41	18.205			7
Mid Ordovician, Llandeilo	1.3.8051	1.5	34.46	22.973			57
Snachez, 1990							
<i>Modiolopsis cuyana</i>	1.8.055	1.5	46.22	30.813			88.5
Mid-Late Ordovician							
Liljedahl, 1983							
<i>Nuculoida lens</i>	3.A.SGU1131	5.3	50.79	9.583			50
Silurian, Upper Wenlockian	3.B.SGU1137	3.5	50.6	14.457			97
	3.C.SGU876	8.3	49.72	5.9904			26
	3.D.SGU886	4.3	50.46	11.735			78.5
	4.E.SGU842	3.4	50.64	14.894			99.5
	4.F.SGU901	3.9	49.64	12.728			90.5
<i>Nuculodonta gotlandica</i>	14.A.SGU1056	3.9	50.77	13.018			89
Mid Silurian, late Wenlockian	14.B.SGU1000	3.6	50.91	14.142			95
	14.C.SGU1026	3.8	50.21	13.213			91
	14.D.SGU1001	4.3	50.25	11.686			71
	17.C.SGU1198	5	49.22	9.844			45.5
	17.E.SGU942	4.3	49.62	11.54			69.5
Liljedahl, 1984							
<i>Janeia silurica</i>	14.A.SGU3608	2.4	51.12	21.3			88.5
Mid Silurian, Late Wenlockian	14.C.SGU3426/3427	1.8	52.69	29.272			100
	14.D.SGU3428/3429	8.9	54.64	6.1393			11.5
<i>Freja fecunda</i>	18.A.SGU3367	5	44.9	8.98			73.5
Mid Silurian, Late Wenlockian	18.H.SGU3461	10	45.94	4.594			36
	18.J.SGU3379	3.7	46.99	12.7			90
Johnston, 1993							
<i>Mytilarca bloomfieldensis</i>	13.A	2.6	43.87	17.044			31
Lower Devonian	13.D	1.8	45.79	24.818			62
	13.F	1.9	37.39	20.027			53
	13.H	1.6	39.08	24.876			62
	13.J	2.1	41.55	20.034			53
	13.M	1.9	60.41	32.548			100

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Johnston, 1993							
<i>Cornellites catellus</i>	22.A	2	53.66	27.142			65
Lower Devonian							
<i>Tolmaia erugisulca</i>	31.A	0.9	47.04	54.761			75.5
Lower Devonian	31.B	0.9	50.4	58.333			87
<i>Goniophora duplisulca</i>	55.A	2.4	52.41	21.471			92
Lower Devonian	55.C	2.9	49.79	17.234			47
	55.H	3.5	52.64	15.083			42.5
<i>Cypricardinia minima</i>	63.A	8.7	44.69	5.1593			83.5
Lower Devonian	63.G	9.1	48.16	5.3098			94
	63.I	9	35.5	3.9261			72
<i>Eoschizodus taemasensis</i>	70.A	2.1	49.45	23.37			78.5
Lower Devonian	no name	1.9	48.78	25.728			86
<i>Crassatellopsis lenticularis</i>	91.A	4	43.52	11.004			53
Lower Devonian	91.C	2.7	36.41	13.435			74
	91.D	4	39.44	9.8625			39.5
	91.E	3.2	38.29	12.048			66.5
	91.G	4.7	37.54	7.9601			14
	91.H	4.8	52.71	11.048			53
	91.I	4.5	50.11	11.116			53
	91.J	2.4	40.94	16.896			94
Miocene-Pliocene Bivalves							
Bird, 1965							
<i>Anadara transversa 1</i>	2.5.UNC3525	2	43.47	21.735			93
Natural Well, North Carolina	2.7.UNC3526	2.2	37.54	17.064			50.5
Duplin Fm.							
Upper Miocene							
<i>Anadara transversa 2</i>	2.4.UNC3527	1.3	37.34	28.723			5.5
Town Creek, North Carolina							
Waccamaw Fm.							
Pliocene							
<i>Anadara transversa 3</i>	2.9.UNC3528	1.2	56.1	46.75			70
James City, North Carolina							
Croatan Fm.							
Pliocene							

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Bird, 1965							
<i>Noetia (Eontia) trigintinaria</i>	2.12.UNC3535	1.5	51.99	34.66			100
Natural Well, North Carolina	2.13.UNC3534	2.1	36.53	17.395			44
Duplin Fm.							
Upper Miocene							
<i>Noetia (Eontia) carolinensis</i>	3.6.UNC3536	1	57.35	57.35			71
Black Rock, North Carolina							
Yorktown Fm.							
Upper Miocene							
<i>Noetia (Eontia) limula</i>	3.1.UNC3537	1	58.77	58.77			84.5
James City, North Carolina							
Croatan Fm.							
Pliocene							
<i>Noetia (Eontia) platyura</i>	3.7.UNC3538	1	60.74	60.74			50.5
Town Creek, North Carolina							
Waccamaw Fm.							
Pliocene							
<i>Glycymeris anteparilis</i>	5.1.UNC3542	0.8	44.38	55.475			100
Silverdale, North Carolina	5.2.UNC3543	1	41.31	41.31			62
Trent Fm.							
Lower Miocene							
<i>Glycymeris americana</i>	4.1.UNC3547	1	77.79	77.79			97.5
Old Dock, North Carolina	5.3.UNC3548	1.2	49.97	41.642			55
Waccamaw Fm.	5.6.UNC3549	1.9	41.03	21.595			17
Pliocene							
<i>Glycymeris subovata</i>	4.3.UNC3550	1	65.51	65.51			100
King's Mill Wharf	5.10.UNC3551	1.5	31.3	20.867			0
Yorktown Fm.							
Upper Miocene							
<i>Glycymeris pectinata</i>	5.7.UNC3554	1.9	33.55	17.658			100
Acme, North Carolina	5.8.UNC3555	1.9	29.01	15.268			94
Waccamaw Fm.							
Pliocene							

FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Amano, 1986						
<i>Glycymeris idensis</i>		18.1b.15028-25	33.8			72
Miocene		18.2b.15028-52	35.7			89
		18.4.15029-15	33.5			69
Lauriate-Rage, 1982						
<i>Astarte omalii omalii</i>		1.1	27.75			55.5
Pliocene		2.3	32.84			82.5
		2.4	27.5			55
		2.5	27.2			52
		2.6	26.7			51.5
		2.7	23.1			24.5
		2.8	30.4			71
		2.9	33.2			83
		3.2	11.2			3.5
		3.3	14.7			6.5
		3.4	22.5			22
		3.5	27.4			54
		3.6	36.2			89.5
		4.1	27.1			52
		4.2	23			24.5
		4.3	24.5			43
		4.4	27.9			56
		4.5	28			59.5
		4.6	31			75.5
		4.7	31.1			75.5
		4.8	33.7			87

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Lauriat-Rage, 1982	1.3			19.4			91
<i>Astarte omalii scalaris 1</i>	7.4			12.1			24.5
(Nantes, France)	7.5			12.1			24.5
	7.6			13.7			38
	7.7			16.6			63.5
	7.8			16.8			66.5
	7.9			19.1			90
	7.10			19.6			93
	7.11			20.6			98
	7.12			20.8			98.5
	7.13			18.9			89
	7.14			16.3			60.5
	7.15			16.6			63.5
	8.1			12.9			31
	8.2			12.1			24.5
	8.3			16.1			57.5
	8.4			18.2			85
	8.5			20.7			98
	8.6			13.1			33.5
	8.7			12.9			30.5
	8.8			12.4			27.5
	8.9			18.9			89
	8.10			17.4			73.5
	8.12			15.1			48.5
	8.13			21			99

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Lauriat-Rage, 1982							
<i>Astarte omalii scalaris 2</i>	1.4			15.5			60
(Angers, France)	5.2			10.4			5.5
	5.3			10.6			6
	5.4			13.5			33
	5.5			16.1			73.5
	5.6			15.6			62
	5.7			18.2			98.5
	5.8			18.3			98.5
	5.9			16.3			76.5
	5.10			14.2			43
	5.11			16.2			75.5
	5.12			15.5			60
	5.13			13.1			26.5
	5.14			16			71.5
	5.15			14			41
	5.17			17			90
	6.1			16.7			84.5
	6.2			17			90
	6.3			14.9			53.5
	6.4			14.9			53.5
	6.5			18			98
	6.6			14.8			51.5
	6.8			11.4			9
	6.9			13.2			27
	6.10			15.7			64
	6.11			16.7			84.5
	6.12			17			90
	6.13			16.5			80.5
	6.14			18.7			100
	6.15			13.5			33
	6.16			15.7			64
	6.17			15.5			60
	6.18			15.8			66.5
<i>Astarte solidula</i>	10.1			16.21			100
	10.2			14.25			100
	10.3			11.98			96.5
	10.4			12.37			97
	10.5			13.2			98.5
<i>Digitaria digitaria 1</i>	14.13			5.9567			85.5
le Pigeon-Blanc	14.14			6.36			99

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Lauriat-Rage, 1982	14.15			4.6767			0
<i>Digitaria digitaria 2</i>							
la Gauviniere							
<i>Astarte fusca incrassata</i>	1.5			16.13			88.5
St. Michel	10.13			14.78			63.5
	10.14			14.96			64
	10.15			17.83			100
	10.16			15.65			87.5
	10.17			15.34			64.5
<i>Astarte sulcata redonensis 1</i>	1.6			16.17			66
St. Michel	11.7			16.15			66
	11.8			16.8			81.5
	11.9			15.82			65.5
<i>Astarte sulcata redonensis 2</i>	11.21			15.58			98
le Houx							
Jung, 1996							
<i>Cardiomya (Cardiomya) islahispaniolae</i>	1.1			9.3	5.4		98.5
late Miocene	1.3			8.4	5.2		84
Dominican Republic	1.4			8.7	5.8		90
	1.6			7.6	4.8		66
	2.1			5	2.9		15.5
	2.3			8	5.3		75.5
<i>Cardiomya (Bowdenia) distira</i>	3.5			3.2	2		73
late Miocene - middle Pliocene	4.1			3	2		57
Dominican Republic	4.3			2.9	2.3		44.5
	4.4			3.3	2.3		91
<i>Plectodon granulatus</i>	2.9			11.3	6.7		52.5
Recent	5.1			10.6	6.4		47.5
Caribbean	6.1			8.8	5.6		17.5
	6.3			11.5	6.5		60
<i>Haliris jamaicensis</i>	9.1			4.3	4.1		81
Pliocene	9.4			4.3	3.9		81
Dominican Republic	10.1			3.2	2.6		29.5

	FIGURED SPECIMENS	MAGNIFICATION	RAW LENGTH (mm)	CALIB. LENGTH (mm)	RAW WIDTH (mm)	CALIB. WIDTH (mm)	PERCENTILE OF BULK SAMPLE (LENGTH)
Jung, 1996							
<i>Trigonulina ornata</i>	11.1			4.2		3.8	88
Recent	11.3			3.4		3.2	36.5
Carribbean	12.1			3.7		3.3	53
	12.3			4		3.6	77.5
<i>Trigonulina pacifica</i>	2.11			4.8		4.2	83.5
Recent	13.1			4.8		4.7	83.5
Santa Catalina Island, California	13.3			4.7		4.3	80
	14.1			5.1		4.9	95.5
	14.3			4.5		4	72
<i>Trigonulina bowdenensis</i>	15.1			3.5		3.1	86.5
late Miocene - mid Pliocene	15.3			3.3		3	82.5
Carribbean	16.1			3.8		3.2	95.5
	16.4			4		3.3	100
	17.1			2.8		2.5	68.5
	17.3			2.1		1.8	27.5
	18.1			2.3		1.9	39
	18.3			2.8		2.6	68.5

Appendix 3.1: Amino Acid Ratios and Dates

SPECIMEN #	SITE	DEPTH (m)	SHELL TYPE	D/L ASPARTIC ACID (ASP)	D/L ASPARTIC ACID (ASP ^{2.6})	D/L ASPARTIC ACID (ASP ^{3.1})	AMS 14C	AGE	FINAL AGE
13001	1	30	Brachiopod	0.095	0.002			-215.265	0.000
13002	1	30	Brachiopod	0.599	0.264		6669	6626.340	6626.340
13003	1	30	Brachiopod	0.322	0.053			1100.998	1100.998
13004	1	30	Brachiopod	0.513	0.176			4338.166	4338.166
13005	1	30	Brachiopod	0.577	0.239			5986.743	5986.743
13006	1	30	Brachiopod	0.600	0.265		6550	6656.326	6656.326
13007	1	30	Brachiopod	0.323	0.053			1112.118	1112.118
13008	1	30	Brachiopod	0.571	0.233			5818.914	5818.914
13009	1	30	Brachiopod	0.491	0.157			3841.530	3841.530
13010	1	30	Brachiopod	0.413	0.100		2539	2351.179	2351.179
13011	1	30	Brachiopod	0.658	0.337			8535.089	8535.089
13012	1	30	Brachiopod	0.578	0.240			6014.988	6014.988
13013	1	30	Brachiopod	0.662	0.342			8674.979	8674.979
13014	1	30	Brachiopod	0.301	0.044			880.052	880.052
13015	1	30	Brachiopod	0.624	0.293			7400.193	7400.193
13016	1	30	Brachiopod	0.479	0.148			3585.180	3585.180
13018	1	30	Brachiopod	0.451	0.126			3025.936	3025.936
13019	1	30	Brachiopod	0.617	0.285			7178.403	7178.403
13021	1	30	Brachiopod	0.321	0.052			1089.933	1089.933
13022	1	30	Brachiopod	0.269	0.033		465	587.922	587.922
13023	1	30	Brachiopod	0.273	0.034			621.594	621.594
13025	1	30	Brachiopod	0.591	0.255			6389.325	6389.325
13026	1	30	Brachiopod	0.514	0.177			4361.571	4361.571
13027	1	30	Brachiopod	0.391	0.087			2003.089	2003.089
13028	1	30	Brachiopod	0.349	0.065			1414.615	1414.615
13029	1	30	Brachiopod	0.600	0.265			6656.326	6656.326
13030	1	30	Brachiopod	0.584	0.247			6186.104	6186.104
13031	1	30	Brachiopod	0.303	0.045			900.073	900.073
91001	9	10	Brachiopod	0.276	0.035			486.197	486.197
91003	9	10	Brachiopod	0.351	0.066			1145.592	1145.592
91004	9	10	Brachiopod	0.194	0.014			30.427	30.427
91005	9	10	Brachiopod	0.473	0.143			2808.346	2808.346
91006	9	10	Brachiopod	0.230	0.022		80	199.491	199.491
91007	9	10	Brachiopod	0.191	0.014			18.368	18.368
91008	9	10	Brachiopod	0.269	0.033			437.128	437.128
91009	9	10	Brachiopod	0.252	0.028			326.229	326.229
91011	9	10	Brachiopod	0.244	0.026			277.996	277.996
91013	9	10	Brachiopod	0.337	0.059			1003.110	1003.110
91014	9	10	Brachiopod	0.564	0.226			4596.007	4596.007
91016	9	10	Brachiopod	0.552	0.213			4331.209	4331.209
91017	9	10	Brachiopod	0.285	0.038			552.276	552.276
91018	9	10	Brachiopod	0.098	0.002		0	-221.814	0.000
91019	9	10	Brachiopod	0.183	0.012			-12.335	0.000
91020	9	10	Brachiopod	0.493	0.159			3149.641	3149.641
91021	9	10	Brachiopod	0.288	0.039			575.060	575.060
91022	9	10	Brachiopod	0.331	0.056			944.864	944.864
91023	9	10	Brachiopod	0.305	0.046			711.473	711.473
91024	9	10	Brachiopod	0.248	0.027			301.801	301.801
91025	9	10	Brachiopod	0.414	0.101			1906.151	1906.151
91026	9	10	Brachiopod	0.176	0.011			-37.497	0.000
91027	9	10	Brachiopod	0.175	0.011			-40.964	0.000
91030	9	10	Brachiopod	0.228	0.021			188.877	188.877
91031	9	10	Brachiopod	0.323	0.053			869.790	869.790

SPECIMEN #	SITE	DEPTH (m)	SHELL TYPE	D/L ASPARTIC ACID (ASP)	D/L ASPARTIC ACID (ASP^2.6)	D/L ASPARTIC ACID (ASP^3.1)	AMS 14C	AGE	FINAL AGE
91032	9	10	Brachiopod	0.534	0.196		3825	3950.948	3950.948
91033	9	10	Brachiopod	0.283	0.038			537.298	537.298
91034	9	10	Brachiopod	0.443	0.120			2325.630	2325.630
91036	9	10	Brachiopod	0.191	0.014			18.368	18.368
91038	9	10	Brachiopod	0.398	0.091			1693.876	1693.876
BB-1	9	10	Brachiopod	0.066	0.001			-254.517	0.000
BB-2	9	10	Brachiopod	0.109	0.003			-205.815	0.000
BB-3	9	10	Brachiopod	0.063	0.001			-257.009	0.000
BB-4	9	10	Brachiopod	0.098	0.002			-221.486	0.000
BB-5	9	10	Brachiopod	0.048	0.000			-265.056	0.000
BB-6	9	10	Brachiopod	0.291	0.040			597.303	597.303
BB-7	9	10	Brachiopod	0.060	0.001			-258.720	0.000
BB-8	9	10	Brachiopod	0.170	0.010			-58.650	0.000
BB-9	9	10	Brachiopod	0.062	0.001			-257.544	0.000
BB-10	9	10	Brachiopod	0.044	0.000			-266.871	0.000
BB-11	9	10	Brachiopod	0.120	0.004			-186.092	0.000
BB-12	9	10	Brachiopod	0.248	0.027			304.678	304.678
BB-13	9	10	Brachiopod	0.226	0.021			176.001	176.001
BB-14	9	10	Brachiopod	0.438	0.117		2522	2251.313	2251.313
BB-15	9	10	Brachiopod	0.340	0.061		784	1035.209	1035.209
BB-16	9	10	Brachiopod	0.289	0.040			585.540	585.540
301	9	10	Brachiopod	0.416	0.102			1938.357	1938.357
376	9	10	Brachiopod	0.459	0.132			2576.398	2576.398
442	9	10	Brachiopod	0.239	0.024			248.093	248.093
543	9	10	Brachiopod	0.426	0.108			2067.954	2067.954
546	9	10	Brachiopod	0.456	0.130			2532.186	2532.186
594	9	10	Brachiopod	0.144	0.007			-132.582	0.000
2	9	10	Brachiopod	0.132	0.005			-161.230	0.000
3	9	10	Brachiopod	0.449	0.125			2423.188	2423.188
4	9	10	Brachiopod	0.225	0.021			173.640	173.640
20	9	10	Brachiopod	0.457	0.131			2549.953	2549.953
158	9	10	Brachiopod	0.241	0.025			259.521	259.521
228	9	10	Brachiopod	0.269	0.033			439.144	439.144
230	9	10	Brachiopod	0.240	0.024			254.957	254.957
236	9	10	Brachiopod	0.333	0.057			965.218	965.218
280	9	10	Brachiopod	0.455	0.129			2505.326	2505.326
281	9	10	Brachiopod	0.490	0.156			3097.634	3097.634
13050	1	30	Bivalve	0.424		0.070		10761.275	10761.275
13051	1	30	Bivalve	0.235		0.011		1641.822	1641.822
13052	1	30	Bivalve	0.308		0.026		3917.733	3917.733
13053	1	30	Bivalve	0.101		0.001		25.519	25.519
13054	1	30	Bivalve	0.178		0.005		630.955	630.955
13055	1	30	Bivalve	0.124		0.002		138.594	138.594
13056	1	30	Bivalve	0.164		0.004		464.576	464.576
13059	1	30	Bivalve	0.215		0.008		1212.141	1212.141
13060	1	30	Bivalve	0.443		0.080		12342.475	12342.475
13061	1	30	Bivalve	0.048		0.000		-89.012	0.000
13062	1	30	Bivalve	0.303		0.025		3712.155	3712.155
13063	1	30	Bivalve	0.098		0.001		14.167	14.167
13064	1	30	Bivalve	0.147		0.003		305.503	305.503
13066	1	30	Bivalve	0.263		0.016		2369.905	2369.905
13067	1	30	Bivalve	0.112		0.001		73.575	73.575
13068	1	30	Bivalve	0.210		0.008		1119.506	1119.506

SPECIMEN #	SITE	DEPTH (m)	SHELL TYPE	D/L ASPARTIC ACID (ASP)	D/L ASPARTIC ACID (ASP^2.6)	D/L ASPARTIC ACID (ASP^3.1)	AMS 14C	AGE	FINAL AGE
13069	1	30	Bivalve	0.365		0.044		6725.188	6725.188
13070	1	30	Bivalve	0.266		0.016		2458.355	2458.355
13071	1	30	Bivalve	0.273		0.018	2808	2657.303	2657.303
13072	1	30	Bivalve	0.168		0.004		508.636	508.636
13073	1	30	Bivalve	0.207		0.008		1074.894	1074.894
13074	1	30	Bivalve	0.235		0.011		1630.348	1630.348
13075	1	30	Bivalve	0.222		0.009	883	1359.844	1359.844
13076	1	30	Bivalve	0.109		0.001		57.147	57.147
13077	1	30	Bivalve	0.075		0.000	0	-52.166	0.000
13078	1	30	Bivalve	0.198		0.007		915.432	915.432
13079	1	30	Bivalve	0.101		0.001		25.519	25.519
13080	1	30	Bivalve	0.137		0.002		225.614	225.614
13081	1	30	Bivalve	0.083		0.000	183	-32.464	0.000
13082	1	30	Bivalve	0.161		0.003		438.164	438.164
13083	1	30	Bivalve	0.190		0.006		793.064	793.064
13084	1	30	Bivalve	0.334		0.033		5083.066	5083.066
13085	1	30	Bivalve	0.205		0.007		1031.399	1031.399
13086	1	30	Bivalve	0.148		0.003		309.812	309.812
13087	1	30	Bivalve	0.119		0.001	222	107.069	107.069
13088	1	30	Bivalve	0.184		0.005	676	708.127	708.127
91042	9	10	Bivalve	0.489		0.109		9562.203	9562.203
91043	9	10	Bivalve	0.138		0.002		177.736	177.736
91044	9	10	Bivalve	0.283		0.020		1745.147	1745.147
91045	9	10	Bivalve	0.366		0.044		3887.821	3887.821
91046	9	10	Bivalve	0.132		0.002		153.327	153.327
91047	9	10	Bivalve	0.329		0.032		2790.632	2790.632
91048	9	10	Bivalve	0.525		0.136		11920.677	11920.677
91049	9	10	Bivalve	0.493		0.112		9807.073	9807.073
91050	9	10	Bivalve	0.493		0.112		9807.073	9807.073
91051	9	10	Bivalve	0.334		0.033		2924.783	2924.783
91052	9	10	Bivalve	0.109		0.001		80.248	80.248
91053	9	10	Bivalve	0.386		0.052		4587.090	4587.090
91054	9	10	Bivalve	0.103		0.001		64.690	64.690
91055	9	10	Bivalve	0.117		0.001		102.793	102.793
91057	9	10	Bivalve	0.373		0.047		4123.709	4123.709
91058	9	10	Bivalve	0.118		0.001		104.825	104.825
91059	9	10	Bivalve	0.365		0.044		3854.886	3854.886
91060	9	10	Bivalve	0.375		0.048		4175.483	4175.483
91061	9	10	Bivalve	0.128		0.002		138.297	138.297
91062	9	10	Bivalve	0.172		0.004	378	363.423	363.423
91063	9	10	Bivalve	0.211		0.008		695.280	695.280
91064	9	10	Bivalve	0.212		0.008		700.488	700.488
91065	9	10	Bivalve	0.132		0.002		151.395	151.395
91066	9	10	Bivalve	0.156		0.003		265.409	265.409
91068	9	10	Bivalve	0.225		0.010		851.113	851.113
91069	9	10	Bivalve	0.440		0.078		6889.614	6889.614
91070	9	10	Bivalve	0.344		0.037		3206.010	3206.010
91071	9	10	Bivalve	0.071		0.000	0	12.286	12.286
91072	9	10	Bivalve	0.074		0.000		15.594	15.594
91073	9	10	Bivalve	0.141		0.002		190.808	190.808
91074	9	10	Bivalve	0.117		0.001		101.786	101.786
91075	9	10	Bivalve	0.317		0.028	2484	2473.534	2473.534
91076	9	10	Bivalve	0.087		0.001		33.492	33.492
91078	9	10	Bivalve	0.304		0.025		2181.675	2181.675
91079	9	10	Bivalve	0.095		0.001		46.748	46.748

Appendix 3.2: Bootstrap program for SAS/IML

This is a balanced bootstrap program for estimating the confidence intervals around the semi-quartile range. The program was written in SAS and SAS/IML (Ver. 9.1) by R. Krause. It is a modified version of a program written by M. Kowalewski (Kowalewski et al., 1998). The program should work in any version of SAS. It requires a data set of raw scores for one variable. The data should be typed or copied into the program where indicated.

```
%let times=5000;          * - enter the desired number of iterations;
data data1;
infile cards;
input var1;
cards;                    * - enter data in the space below (between "cards" and the floating semi colon);

;
PROC UNIVARIATE data=data1 noprint;
  var var1;
  output out=initial n=n std=std pctlpre=p pctlpts=25 75;
PROC PRINT data=initial;

PROC IML;
USE data1;
READ ALL INTO X;

*** MODULE 'RANVEC' creates a new vector 'v_out' by resampling without replacement the input vector 'in';
START ranvec(in,v_out);
  k=nrow(in);
  v_index=in;
  do i=1 to k;
    rand=floor((k-i+1)*ranuni(0) + 1);
    v_ran=v_index[v_index[rand]];
    v_index=remove(v_index,rand);
  end;
  v_out=v_ran;
FINISH ranvec;

*** MODULE 'MIXUP' creates a template of row and column ids for balanced-bootstrap resampling;
START mixup(X,times,template);
  n=nrow(X);
  template=t(1:n)*j(1,times,1);
  do i=1 to times;
    run ranvec(template[,i],out);
    template[,i]=t(out);
  end;
  do i=1 to n;
    run ranvec(t(template[i,]),out);
    template[i,]=out;
  end;
FINISH mixup;

*** MODULE 'RANDOM' invokes other modules and executes a simulation;
START random(X,times,out);
  quar=quartile(X);      *calculates actual semiquartile range;
  q1=quar[2,];
  q3=quar[4,];
  asqr=(q3-q1)/2;
  print 'Actual semi-quartile range of sample =' asqr;
  run mixup(X,times,template);
```

```

do i=1 to times;
  Y=X[template[,i]];
  quar=quartile(Y);
  q1=quar[2,];
  q3=quar[4,];
  sqr=(q3-q1)/2;
  r=sqr;
  fin=fin//r;
end;
bsqr=sum(fin)/&times;
print 'Mean bootstrap semi-quartile range =' bsqr;
diff=bsqr-asqr;
print 'The difference between them is ' diff;
corr=j(&times,1,bsqr-asqr);
fin2=fin-corr;
out=fin2;
FINISH random;

run random(X,&times,out);
create new from out;
append from out;
close new;
quit;

PROC UNIVARIATE data=new noprint;
  var coll;
  output out=result mean=mean n=iter pctlpre=p pctlpts=0.5 2.5 97.5 99.5;
PROC PRINT;
run;
quit;

```

Appendix 3.3: Completeness simulation in SAS

This program simulates the effects of sampling from an exponential distribution on completeness estimates. It was written in SAS (Ver. 9.1) by R. Krause, and is based on a similar program written by M. Kowalewski (Kowalewski et al., 1998). It should work in any version of SAS. The program is designed for $r = 100$ ($r = \text{resolution/binning}$). To change r , the module “data random” must be modified. The program used to simulate a uniform distribution is given in Kowalewski et al. (1998).

```
* ENTER MACROVARIABLES AND LABELS *;
%let n=36;                * define sample size *;
%let times=1000;         * number of iterations *;
%let range=12342;        * age range within the sample *;
%let complet=.185;       * the actual completeness of the sample *;
%let expparam=.1;        * the rate parameter (lamda) of the exponential distribution;
title1 *simulation of sampling effect on within-sample completeness of the record*;
title2 *based on resampling an exponential distribution*;
title3 *age range=&range, n=&n, actual completeness=&complet iterations=&times*;
options pagesize=10000;

* SAS PROGRAM (NO MODIFICATIONS ARE REQUIRED) *;
data random;
  do j=1 to &times;
    do i=1 to &n;
      k=&range*(ranexp(0)/&expparam);
      w=floor(k/100)*100;      *w=shell age;
      if w>&range then v=floor(&range/100)*100;
      else v=w ;
      output;
    end;
  end;
keep k j w v;

PROC UNIVARIATE data=random noprint;
  var w;
  output out=test n=n max=maxw pctlpre=p pctlpts=95 99;
run;
PROC PRINT data=test;

PROC FREQ data=random noprint;
  by j;
  tables v /out=a;
run;

PROC UNIVARIATE data=a noprint;
  var v;
  by j;
  output out=b n=n;
run;

data final;
  set b;
  z=n/(&range/100);
  if z>=&complet then y=1;
  else y=0;
  keep z y;
run;
```

```

PROC PRINT;
Title4'the expected sample completeness and its 95 and 99 confidence intervals';

PROC UNIVARIATE data=final noprint;
  var z;
  output out=result mean=mean n=iter pctlpre=p pctlpts=0.5 2.5 97.5 99.5;
PROC PRINT;
run;

PROC UNIVARIATE data=final noprint;
  var y;
  output out=result2 sum=p;
run;
Title5'Probability that the original sample came from 100%-complete, exponentially distributed record';
Title6'probA = the probability of greater completeness than actual';
Title7'probB = the probability of lesser completeness than actual';

data prob;
  set result2;
  probA=p/&times;
  probB=1-probA;
PROC PRINT;
run;
quit;

```