BODY SIZE ESTIMATES FROM THE LITERATURE: UTILITY AND POTENTIAL FOR MACROEVOLUTIONARY STUDIES

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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. It is possible, however, that images of specimens represent a biased sample of the fossil record. Thus, the quality of these data must be assessed before body size estimates from the literature can be used in analyses.

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 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

The purpose of this paper is to investigate the biases inherent in the collection of simple linear measurements from published images. Despite their promise, data derived from images may be biased in several ways, depending on the type of information being extracted. Specifically, the quality of these data will be assessed with respect to three parameters: (1) bias direction—the presence of nonrandom 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 un-

derstanding of these bias parameters will it be possible to assess the utility of monograph-derived size data.

Images of specimens are essential to the taxonomic literature. They enable workers 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 described. For this reason, taxonomically focused journals often require high-quality images to accompany any description of a new species, and images are highly encouraged in papers not focused on alpha-taxonomy as well (Paleontological Society, 2006, Journal of Paleontology Instructions for Authors, http://www.journalofpaleontology.org/instruct.htm, checked July 2006). 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 the central importance of published images of specimens in alpha-taxonomy, paleontologists have underutilized them in the analysis and synthesis of existing taxonomic information. In the last few decades, some 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, 1992, 2002; Benton, 1993) have used 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 is just beginning to be explored in large, community-wide initiatives like the Paleobiology Database (http://paleodb.org, checked September 2006). 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 traditionally considered specimen based. For example, published images can yield a wealth of morphological information, from simple linear dimensions to landmark coordinates for geometric morphometric analysis, because taxonomists take great care to visually document all diagnostic features of a species.

The inclusion of image-derived data in a study is advantageous 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 reposited 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), which closely approximates the level of detail available in a museum or field collection.

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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 failure to report magnification accurately.

While it is difficult to address each problem separately, several studies have addressed this issue by evaluating the concordance of measurements of specimens and their images. Kowalewski et al. (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. Studies 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) 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 than their actual size in images. 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. 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 monographs.

METHODS

To test for size bias in the monographs (Table 1), 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 1). Since each of these species localities was treated as a separate sample by the original authors and since we are not concerned with phylogenetic effects in this study, each discrete species locality will hereafter be referred to and treated 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. In most cases, however, 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 in the Paleozoic group, and Paleocene and Eocene specimens were placed in the Cenozoic group. For bivalves, Ordovician through Devonian specimens were placed in 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, size of the bulk sample for a species, and number of figured specimens for a species 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 linear measurement as a proxy for size of each specimen. This is a reasonable procedure because simple linear measurements are highly correlated with body mass, diameter, and other size measures in most organisms (Niklas, 1994). The measurements used are the standard dimensions for each group and should be familiar to most workers (Fig. 1). For brachiopods, we used the length of the ventral valve, which is defined as the maximum dimension that is coincident with the medial symmetry plane. For bivalves, height was used, which 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 1). The counterpart, or bulk sample, consisted of length 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 the bulk samples used in this study came from tables or scatter plots of raw measurements reported in 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.

Data was extracted from scatter plots using the digitizing software, DigitizeIt, which is available as shareware (Bormann, 2003). Images of each published plot were scanned at 600 dpi and points were digitized manually after calibration of the axes. The accuracy and precision of this method were evaluated in a pilot study in which a single point on a published scatter-plot was digitized ten separate times. Each time, the image of the plot was reloaded into the DigitizeIt program and the axes were recalibrated. The results of the pilot study indicate that the average deviation of digitized points from the actual value (reported by the original author) was 0.19 mm. The magnitude of this error can be considered negligible since many measurements were only reported to the nearest millimeter. The precision of the method was evaluated using the standard deviation of all digitized estimates, which was 0.03 mm. This level of precision was deemed adequate for this study.

All statistical analyses were performed with codes written by MK and RAK with Statistical Analysis Software (SAS) and Interactive Matrix Language (SAS/IML) version 9.1.3 (SAS Institute, 2002). 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. 2A). 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. 2A). 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. 2B). 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. If, however, the percentile-frequency

TABLE 1—Attributes of bulk sample and monograph sample for each species. Bulk sample: n_{bulk} = number of specimens measured by monograph author; n_{total} = total number of specimens available from a particular sample; when unreported, this category is scored as "-". Monograph sample: n_{mon} = 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.

Species	n_{mon}	n_{bulk}	n_{total}	Period	Ref.	Region
Brachiopods						
Adairia adairensis	2	24	117	M	10	Ozark region, USA
Antirhynchonella thomasi	9	29	200	S	3	Ozark region, USA
Atrypina erugata	5	19	50	S	3	Ozark region, USA
Basiliola sp.	3	15	—	P	9	Carnarvon Basin, w. Australia
Biernatella lentiformis	7	103	—	D	5	Holy Cross Mtns., Poland
Biernatella ovalis	4	15	—	D	5	Holy Cross Mtns., Poland
Biernatella polonica	1	26	—	D	5	Holy Cross Mtns., Poland
Dicamaropsis parva	13	93	200	S	3	AR and OK, USA
Dicoelosia bilobella	5	33	100	S	3	AR and OK, USA
Dicoelosia oklahomensis	3	13	—	S	3	AR and OK, USA
Eospirifer acutolineatus acutolineatus	5	29	100	S	3	AR and OK, USA
Eospirifer acutolineatus pentagonus	6	30	300	S	3	AR and OK, USA
Giraliathgyris kaitrinae	2	54	—	P	9	Carnarvon Basin, w. Australia
Giraliathyris jubileensis	3	44	—	E	9	Carnarvon Basin, w. Australia
Giraliathyris mcnamarai	1	81	—	P	9	Carnarvon Basin, w. Australia
Hircinisca havliceki	4	22	45	S	3	AR and OK, USA
Inflatia cherokeensis	2	48	100	M	10	Ozark region, USA
Inflatia clydensis	2	12	102	M	10	Ozark region, USA
Inflatia cooperi	2	15	42	M	10	Ozark region, USA
Inflatia gracilis	1	12	32	M	10	Ozark region, USA
Inflatia inflata	2	27	40	M	10	Ozark region, USA
Inflatia pusilla	1	24	165	M	10	Ozark region, USA
Kozlowskiellina (K.) vaningeni	6	47	200	S	3	AR and OK, USA
Meristina clairensis	3	21	60	S	3	AR and OK, USA
Nanospira clairensis	11	67	200	S	3	AR and OK, USA
Nucleospira lens	1	36	645	D	15	Arctic Canada
Oepikina minnesotensis	26	80	—	O	18	northern KY, USA
Oepikina minnesotensis	13	94	—	O	18	northern KY, USA
Orthorhynchula linneyi	3	38	—	O	11	northern KY, USA
Orthorhynchula sublinneyi	7	39	—	O	11	northern KY, USA
Pionomena recens	10	65	—	O	18	northern KY, USA
Platystrophia annieana	4	33	—	O	1	northern KY, USA
Platystrophia colbienesis	4	14	—	O	1	northern KY, USA
Platystrophia elegantula	1	10	—	O	1	northern KY, USA
Platystrophia ponderosa	7	34	—	O	1	northern KY, USA
Plicatoria wilmingtonensis	25	80	251	E	8	Wilmington, NC, USA
Plicatoria wilmingtonensis	8	235	235	E	8	Wilmington, NC, USA
Rhyncotrema increbescens	7	29	—	O	11	northern KY, USA
Sowerbyella sp.	5	23	—	O	11	northern KY, USA
Terebratulina lachryma	1	24	24	E	8	SC, USA
Terebratulina wilsoni	2	48	48	E	8	SC, USA
Victorithyris blakeorum	4	39	—	P	9	Carnarvon Basin, w. Australia
Victorithyris decapello	2	54	—	P	9	Carnarvon Basin, w. Australia
Waiotrypa sulcicarina	3	31	—	D	6	Holy Cross Mtns., Poland
Bivalves						
Anadara transversa	2	54	—	Mio.	7	Natural Well, NC, USA
Anadara transversa	1	20	—	Plio.	7	Town Creek, NC, USA
Anadara transversa	1	20	—	Plio.	7	James City, NC, USA
Astarte fusca incrassata	6	50	—	Plio.	14	St. Michel, Pays de la Loire. France
Astarte omalii omalii	21	29	—	Plio.	14	Nantes, Pays de la Loire, France
Astarte omalii scalaris	25	176	—	Plio.	14	Nantes, Pays de la Loire, France
Astarte omalii scalaris	33	128	—	Plio.	14	Angers, Pays de la Loire, France
Astarte solidula	5	100	—	Plio.	14	Nantes, Pays de la Loire, France
Astarte sulcata redonensis	4	50	—	Plio.	14	St. Michel, Pays de la Loire, France
Astarte sulcata redonensis	1	51	—	Plio.	14	le Houx, Pays de la Loire, France
Cadomia typa	2	16	16	O	19	western Argentina
Cardiomya (C.) islahispaniolae	6	25	—	Mio.	13	Dominican Republic
Cardiomya (Bowdenia) distira	4	28	—	Mio.-Plio.	13	Dominican Republic
Comellites catellus	1	14	34	D	12	southeastern Australia
Crassatellopsis lenticularis	8	15	15	D	12	southeastern Australia
Cypricardinia minima	3	18	18	D	12	southeastern Australia
Digitaria digitaria	2	68	—	Plio.	14	le Pigeon-Blanc, Pays de la Loire, France
Digitaria digitaria	1	38	—	Plio.	14	la Gauviniere, Pays de la Loire, France
Eoschizodus taemasensis	2	14	18	D	12	southeastern Australia
Freja fecunda	3	65	164	S	17	Gotland, Sweden

TABLE 1—Continued.

Species	n_{mon}	n_{bulk}	n_{total}	Period	Ref.	Region
Glycymeris americana	3	40	—	Plio.	7	Old Dock, NC, USA
Glycymeris anteparilis	2	21	—	Mio	7	Silverdale, NC, USA
Glycymeris idensis	3	50	—	Mio.	2	Hokkaido, Japan
Glycymeris pectinata	2	20	—	Plio.	7	Acme, NC, USA
Glycymeris subovata	2	21	—	Mio.	7	James River, VA, USA
Goniophora duplisulca	3	27	29	D	12	southeastern Australia
Gotodonta gotlandica	4	62	214	S	22	Gotland, Sweden
Haliris jamaicensis	3	10	—	Plio.	13	Dominican Republic
Janeia silurica	3	18	597	S	17	Gotland, Sweden
Modiolopsis cuyana	1	17	17	O	20	western Argentina
Myoplusia contrastans	4	17	35	O	4	Crozon, France
Mytilarca bloomfieldensis	6	13	18	D	12	southeastern Australia
Noetia (*Eontia*) *carolinensis*	1	20	—	Mio	7	Black Rock, NC, USA
Noetia (*Eontia*) *limula*	1	20	—	Plio	7	James City, NC, USA
Noetia (*Eontia*) *platyura*	1	20	—	Plio	7	Town Creek, NC, USA
Noetia (*Eontia*) *trigintinaria*	2	16	—	Mio	7	Natural Well, NC, USA
Nuculites argentinum	7	19	25	S	21	western Argentina
Nuculodonta gotlandica	6	197	218	S	16	Gotland, Sweden
Nuculoida lens	6	142	153	S	16	Gotland, Sweden
Plectodon granulatus	4	20	—	R	13	Caribbean Sea
Similodonta djupvikensis	1	15	26	S	22	Gotland, Sweden
Trigonulina bowdenensis	8	54	—	Mio.-Plio.	13	Dominican Republic
Trigonulina ornata	4	74	—	R	13	Carribean Sea
Trigonulina pacifica	5	155	—	R	13	Santa Catalina Island, CA, USA

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. 2C). Specific groups of species were then compared through a series of simple scatter plots (Fig. 2D).

Figure 3 depicts a series of null-models for this analysis. It is not an exhaustive list of the possible null models, but rather an attempt to illustrate some of the more likely scenarios that may be encountered. In the best-case scenario (Fig. 3A), 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 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 3B. Here, monographed specimens show a slight size bias with respect to the average size of bulk sample specimens. The magnitude of the size bias is consistent from species to species regardless of size, however, 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 are still useful because the bias is consistent and easily corrected for all species across a wide size range.

A third model (Fig. 3C) 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

FIGURE 2—Construction of 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–D) Species-level analysis: mean of bulk size-frequency distribution for a species is compared to mean size of monographed specimens for that species with simple scatter plots of bulk mean versus monograph mean.
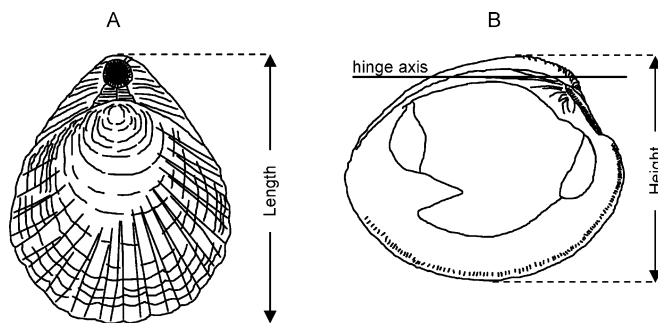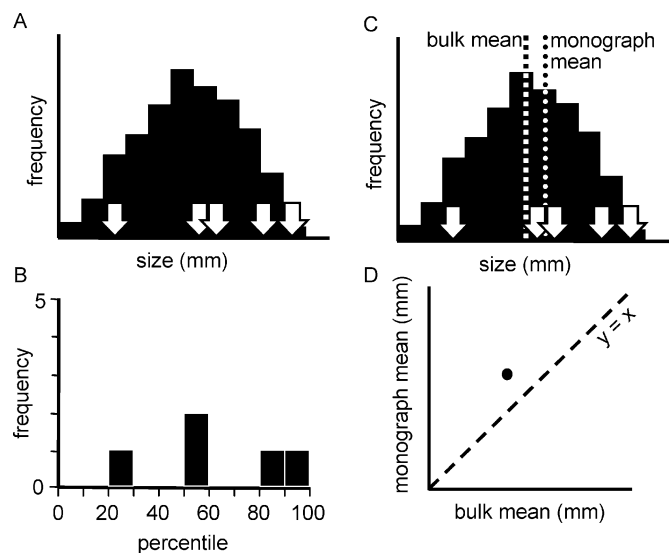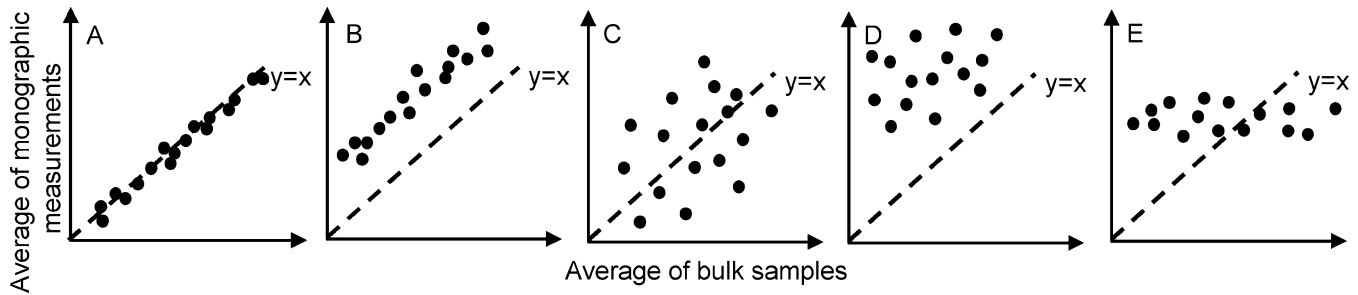

FIGURE 1—Illustration of measurements used in this study. See text for descriptions. A) Length of ventral valve for brachiopods. B) Height for bivalves.

FIGURE 3—Null models for species-level analysis. A) Images in monographs are not biased with respect to bulk sample. B) Images in monographs are biased but magnitude of bias is similar for all species across a wide size range. C) Some species exhibit a monographic size bias, while 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.

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 (Fig. 3D) 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 fifth model (Fig. 3E) depicts a scenario in which it is possible that the size of monographed specimens could vary linearly, or in some more complex fashion, from 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.

RESULTS

Specimen-Level Analysis

The percentile-frequency distributions (Fig. 4) summarize the results from the specimen-level analysis. Each group of the data displays a markedly left-skewed distribution, which indicates that the majority (~75%) of monograph images in each group have sizes that fall well above the 50th percentile for a given species' bulk-collected size-frequency distribution (Table 2). In fact, the means of these distributions are tightly constrained between the 65th and 69th percentile, and their standard deviations (SD) show no clear trend (Fig. 5; Table 2, first set of rows). Furthermore, when 95% confidence intervals are applied to the mean and SD for these distributions, it is clear that they are indistinguishable from each other (Fig. 5). Statistical comparisons of the distributions also show no significant difference in central tendency or distribution shape (Table 3).
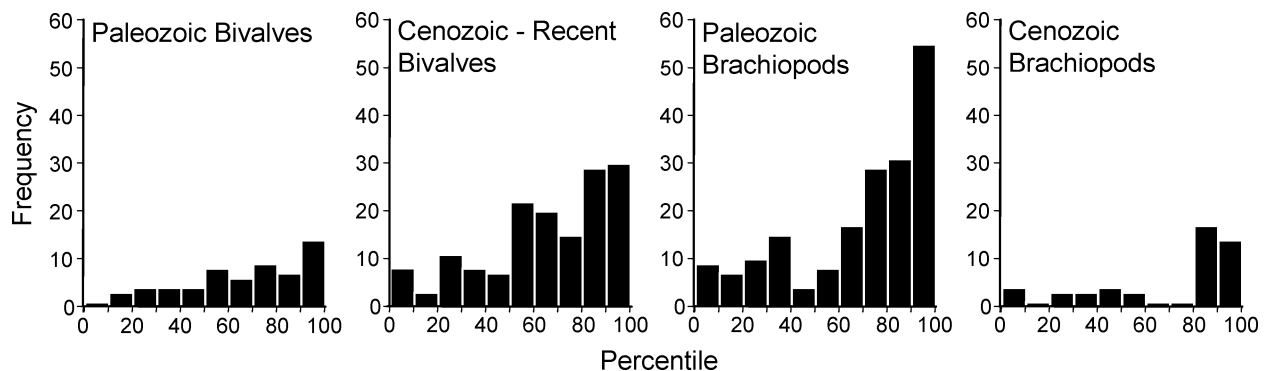
Species-Level Analysis

In all cases, the scatter plots from the species-level analysis (Fig. 6) resemble the null model for biased yet predictable monographic measurements (Fig. 3B), because the slopes of the least-squares regression lines are close to unity, and the R-squared values are high and significant (Table 4). Although logarithmic axes were used on each of the plots in Figure 7 as is appropriate for body size measurements, regressions were completed on both raw and log-transformed data and showed similar results (Table 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 4).

Another way to visualize the amount of bias in a particular group is through the inset plots of residuals in Figure 6. Residuals were calculated from the line of equality rather than from the least-squares regression line. Thus, a residual equal to zero in Figure 6 indicates a species with a monograph mean and bulk sample mean that are exactly equal to each other. The residuals plots (Fig. 6) show that for each group of the data, the majority of species had monograph means that were larger than their counterpart bulk-sample mean.

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. 7) are similar to those shown earlier (Fig. 4) and

FIGURE 4—Percentile-frequency distributions.

TABLE 2—Basic statistics for percentile distributions derived from specimen-level analysis. N = sample size; SD = standard deviation; Min. = minimum value; Max. = maximum value; Q1 = 25th percentile of the distribution; Q3 = 75th percentile of the distribution; Skew. = skewness; Kurt. = kurtosis.

	N	Mean	Median	SD	Min.	Max.	Q1	Q3	Skew.	Kurt.
All monograph measurements	449	67.3	74.0	28.0	0.0	100.0	50.0	90.5	−0.72	−0.59
Bivalves	213	65.3	69.0	27.0	0.0	100.0	50.5	89.0	−0.6	−0.58
Brachiopods	236	69.0	80.0	28.8	1.0	100.0	46.5	92.0	−0.85	−0.52
Paleozoic bivalves	60	65.1	70.3	26.6	7.0	100.0	48.5	89.5	−0.54	−0.72
Cenozoic-recent bivalves	153	65.4	68.5	27.3	0.0	100.0	50.5	89.0	−0.62	−0.51
Paleozoic brachiopods	185	69.3	78.0	28.4	1.0	100.0	53.5	92.5	−0.85	−0.47
Cenozoic brachiopods	51	68.2	81.5	30.4	3.0	100.0	43.5	92.0	−0.85	−0.66
Regional distributions										
Bivalves: U.S. and Caribbean	52	67.2	72.5	27.2	0.0	100.0	50.5	89.0	−0.77	−0.26
Bivalves: Europe	125	65.1	66.5	27.8	0.0	100.0	48.5	90.0	−0.55	−0.74
Bivalves: Other	36	63.2	65.8	24.3	7.0	100.0	53.0	83.8	−0.65	−0.07
Brachiopods: U.S.	205	68.3	78.5	29.5	1.0	100.0	44.0	92.5	−0.81	−0.6
Brachiopods: Other	31	74.0	83.0	23.6	24.0	100.0	59.0	91.0	−0.99	−0.33
Year-of-publication distributions										
Bivalves: 1960s–1970s	27	64.9	70.0	32.2	0.0	100.0	44.0	94.0	−0.56	−0.89
Bivalves: 1980s	121	65.0	66.5	27.7	0.0	100.0	50.0	89.0	−0.6	−0.6
Bivalves: 1990s	65	65.9	72.0	23.6	10.5	100.0	53.0	84.0	−0.59	−0.48
Brachiopods: 1960s	70	71.3	83.0	27.9	2.5	100.0	56.0	92.5	−1.03	−0.15
Brachiopods: 1970s	87	66.8	73.0	30.4	1.0	100.0	40.0	94.0	−0.71	−0.74
Brachiopods: 1980s	36	65.6	81.5	32.2	3.0	100.0	40.3	90.0	−0.77	−0.85
Brachiopods: 1990s–present	43	72.6	82.5	23.8	24.0	100.0	54.0	91.0	−0.82	−0.71
Bulk sample size										
Bivalves: n = 1–25	64	63.0	66.25	28.5	0.0	100.0	49.0	85.3	−0.57	−0.63
Bivalves: n = 26–50	45	60.4	64	25.4	0.0	100.0	51.5	81.5	−0.7	0.01
Bivalves: n = 51–150	68	68.9	74.5	27.2	5.5	100.0	51.0	93.5	−0.67	−0.6
Bivalves: n = 151–200	36	68.7	72.75	25.6	24.5	99.0	47.0	90.5	−0.56	−1.12
Brachiopods: n = 1–25	41	74.7	82	24.0	9.0	100.0	61.0	90.5	−1.24	1.13
Brachiopods: n = 26–50	77	65.8	78	32.4	1.0	100.0	36.0	95.0	−0.57	−1.15
Brachiopods: n = 51–80	76	68.2	76.25	27.8	4.0	100.0	48.0	91.0	−0.79	−0.53
Brachiopods: n = 81–250	42	71.0	81.25	27.8	3.0	100.0	64.0	89.5	−1.24	0.35
Monograph sample size										
Bivalves: n = 1	11	58.6	70.0	37.0	0.0	100.0	11.5	88.5	−0.67	−1.11
Bivalves: n = 2–5	70	70.1	76.8	26.2	0.0	100.0	53.0	93.0	−0.82	−0.16
Bivlaves: n = 6–10	53	67.9	69.5	24.7	10.5	100.0	53.0	89.0	−0.63	−0.41
Bivalves: n > 10	79	60.2	60.5	27.1	3.5	100.0	38.0	84.5	−0.34	−0.86
Brachiopods: n = 1	7	49.8	46.0	30.0	10.0	100.0	24.0	73.0	0.50	0.11
Brachiopods: n = 2–5	74	78.4	86.0	22.9	9.0	100.0	72.0	95.0	−1.38	1.15
Brachiopods: n = 6–10	67	62.0	73.0	32.1	1.0	100.0	32.0	89.0	−0.49	−1.16
Brachiopods: n > 10	88	68.0	78.0	28.5	4.0	100.0	48.0	91.3	−0.85	−0.51

are not significantly different from each other (Fig. 8; Table 5). The sample size for non–U.S. brachiopods, however, may not be sufficient to make such a comparison. A similar result holds for species-level analysis of the regional data (Fig. 9). The two plots of Figure 9 have a strong resemblance to Figure 6 and to the null model for biased but predictable monograph data (Fig. 3B). 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 9, inset plots). The statistical parameters for each least-squares regression show highly significant R-squared values with all slopes near unity (Table 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. 10) bear a striking resemblance to the pattern shown earlier in Figure 4. These
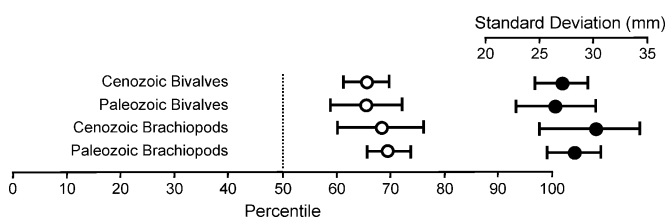

FIGURE 5—Means (open circles) and standard deviations (filled circles) of percentile-frequency distributions. 95% confidence intervals estimated by separate, 1000 iteration bootstrap simulations.

TABLE 3—Percentile distribution comparisons for primary data groups. Because of multiple pairwise comparisons, the Bonferroni correction must be applied and the significance criterion α must be 0.05/4 = 0.0125.

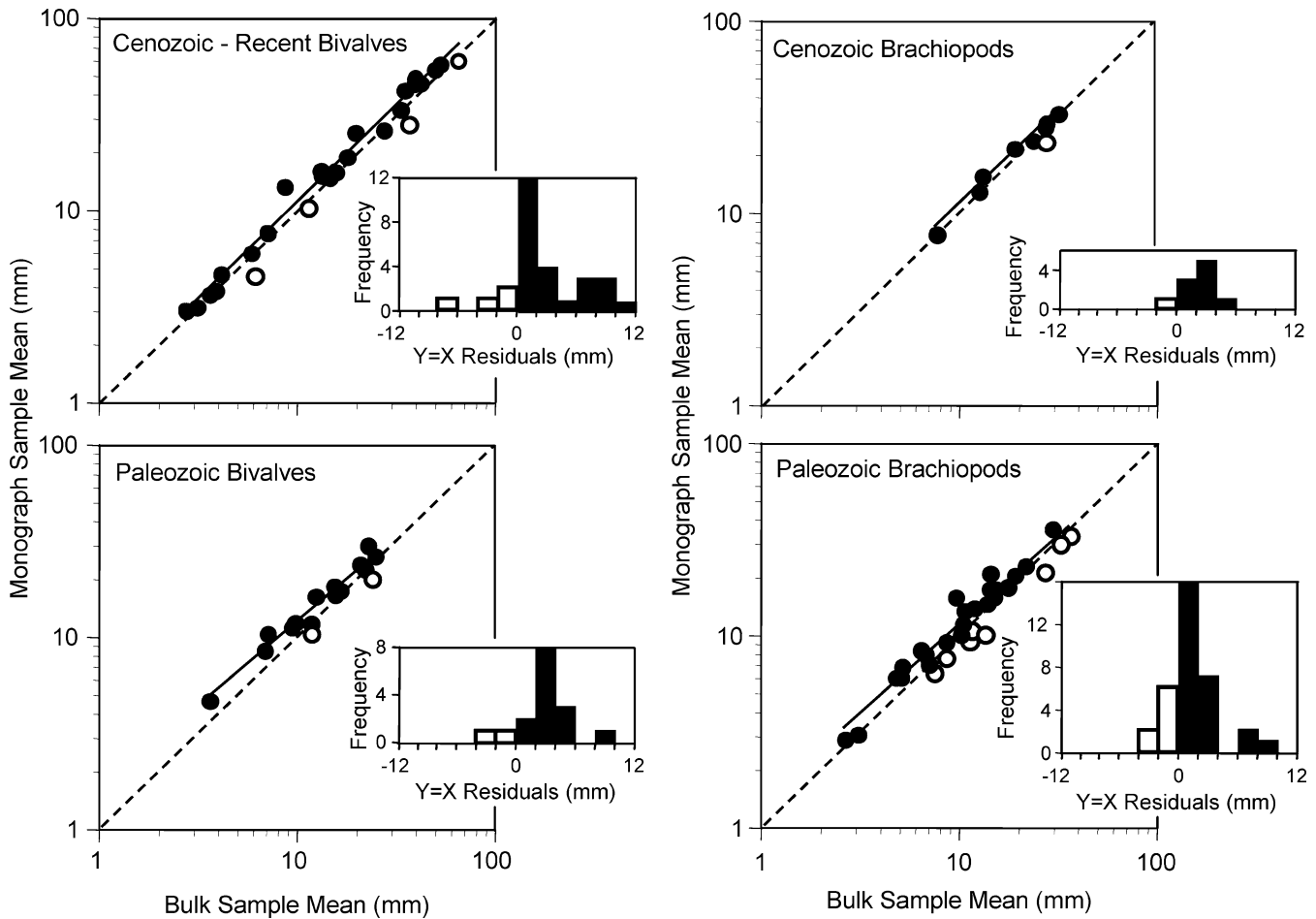|	Wilcoxon two-sample test		Kolmogorov-Smirnov Two-sample test	
	Z	p	D	p
Bivalves: Paleozoic-Cenozoic	−0.116	0.908	0.08	0.945
Brachiopods: Paleozoic-Cenozoic	−0.016	0.987	0.148	0.342
Paleozoic: Bivalves and brachiopods	−1.434	0.152	0.147	0.279
Cenozoic: Bivalves and brachiopods	0.923	0.356	0.229	0.036

FIGURE 6—Scatter plots with least-squares regressions show results of species-level analysis. Statistical parameters associated with these regressions given in Table 4. Inset plots show residuals computed from line of equality. Open symbols and white columns indicate monograph data biased in a negative direction with respect to bulk sample.

TABLE 4—Statistical parameters of regressions from species-level analysis. Regressions 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	−0.1	0.97	<0.001	0.98	0.06	0.97	<0.001
Year-of-publication distributions									
Bivalves: 1960s–1970s	14	1.02	4.01	0.92	<0.001	0.89	0.23	0.93	<0.001
Bivalves: 1980s	15	0.96	2.33	0.93	<0.001	0.92	0.15	0.88	<0.001
Bivalves: 1990s	15	1.23	−0.61	0.97	<0.001	1.01	0.05	0.98	<0.001
Brachiopods: 1960s	11	1.29	−0.25	0.85	<0.001	1.04	0.05	0.91	<0.001
Brachiopods: 1970s	11	0.72	5.25	0.64	0.002	0.71	0.38	0.73	0.001
Brachiopods: 1980s–2000s	22	1.07	0.37	0.95	<0.001	0.98	0.06	0.97	<0.001
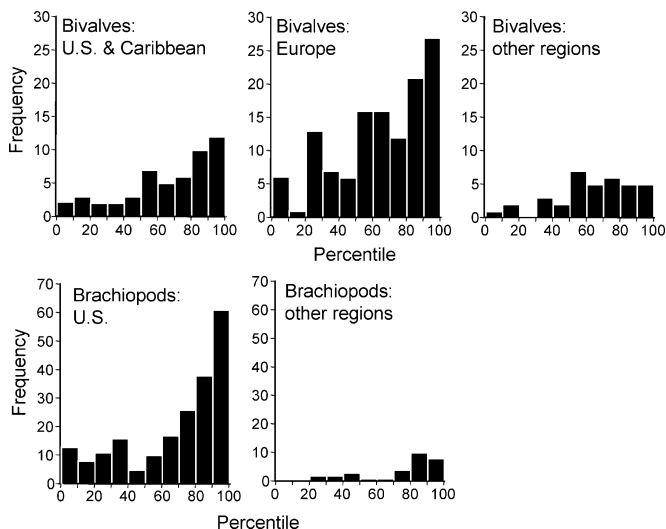
FIGURE 7—Percentile-frequency distributions for bivalves and brachiopods grouped by region from which monograph material was collected.
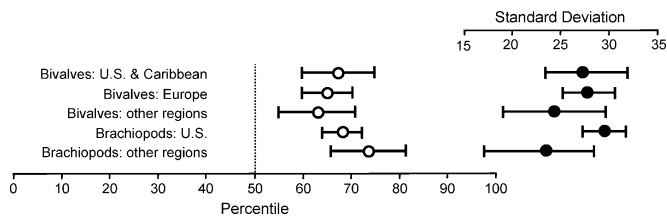

FIGURE 8—Means (open circles) and standard deviations (filled circles) of percentile-frequency distributions grouped by geographical region. 95% confidence intervals computed with separate, 1000 iteration bootstrap simulations.

distributions are also not significantly different from each other (Fig. 11; Table 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. 12).

Sample Size.—The effect of the sample size on the bias can be studied in two ways. The size of the bulk sample is important to note because it reflects the number of specimens that were available to the author at the time of publication. If an author is in possession of only a small number of specimens ($\leq$10) of a species, then, in a sense, the exemplars of that species to be imaged in a publication have been preselected during collection. If, however, 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. The size of the monograph sample is also important, because it is the number of specimens that the author ultimately chose to figure for a publication. Since the monograph sample is always much smaller than the bulk sample for a given species, the size of the monograph sample may be expected to have more of an effect on the bias pattern.

Both sample sizes have been used as grouping variables in a specimen-level analysis. Both bulk and monograph sample size groups for each clade are rather arbitrary and were chosen so that the data was divided as evenly as possible (Fig. 13; Table 2). The only exception is where the monograph sample size is equal to 1. Clearly, there are many fewer specimens for bivalves and brachiopods in this group than there are for the other groups, but this grouping was used so that the monographic bias resulting from only one figured specimen could be observed. The histograms in Figure 13 clearly indicate the same type of monographic bias illustrated earlier, and these distributions are, for the most part, statistically indistinguishable from each other (Table 5). The only exceptions are the brachiopod distributions grouped by monograph sample size. At least one of these distributions is different from the others as determined by the Kruskal-Wallis Test.

The results of the species-level analysis for data grouped by sample size were plotted differently than previous analyses so that sample size could be treated as an integer variable rather than as discrete groups. Figure 14 includes four plots, one each for the monograph sample size and the bulk sample size for bivalve and brachiopod species, each plotted against a metric called percent difference (Fig. 14). 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. As expected, most species plot above the line of zero difference—this is the expression of the monographic bias. All four plots show rather wide scatter at small sample sizes and somewhat less scatter at large sample sizes. The dependence of percent difference on each of the sample sizes was assessed via two nonparametric tests of association: Spearman's r and Kendall's τ. The results of these tests, shown within each plot, indicate that there is generally no significant relationship between percent difference and sample size. The exception is, again, the monograph sample size for brachiopods, which shows a significant positive correlation with both measures of association (Fig. 14). Thus, monograph sample size may have a significant effect on the pattern of the monographic bias, whereas bulk sample size does not.

DISCUSSION

Characterization of Bias

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

The uniformity of the direction and magnitude of bias obtained from specimen-level analysis is striking (Figs. 4–5). 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. A representative sample of specimens must first be assembled in order to adequately describe any species (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.

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

TABLE 5—Percentile distribution comparisons for data grouped by region, year of publication, and bulk and monograph 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: Bulk sample size comparisons	4.67	0.20
Bivalves: Monograph sample size comparisons	6.20	0.10
Brachiopods: Regional comparisons	0.48	0.49
Brachiopods: Year-of-publication comparisons	1.08	0.78
Brachiopods: Bulk sample size comparisons	1.19	0.76
Brachiopods: Monograph sample size comparisons	13.74	0.003
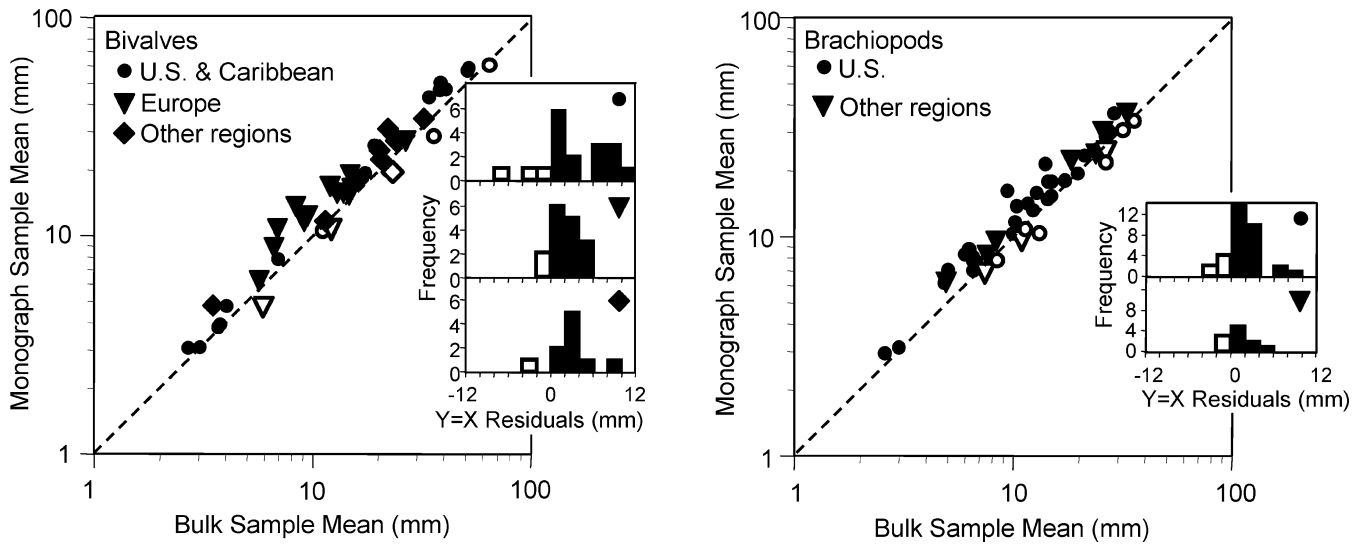
FIGURE 9—Scatter plots with least-squares regressions show results of species-level analysis with data grouped by geographical region. Statistical parameters associated with these regressions given in Table 4. Inset plots show residuals computed from line of equality. Open symbols and white columns indicate monograph data biased in a negative direction with respect to bulk sample.

would be greater. Figure 5 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). 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. 6) indicate a close resemblance to the scenario illustrated by Figure 3B. 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. 6; Table 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.

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. One possibility is that the monographic bias is caused by a factor not controlled for in this analysis. It is difficult to conceive of a factor that imposes such a consistent bias on the data, but methodological biases may be worth exploring in more detail in future studies. For example, a process similar but
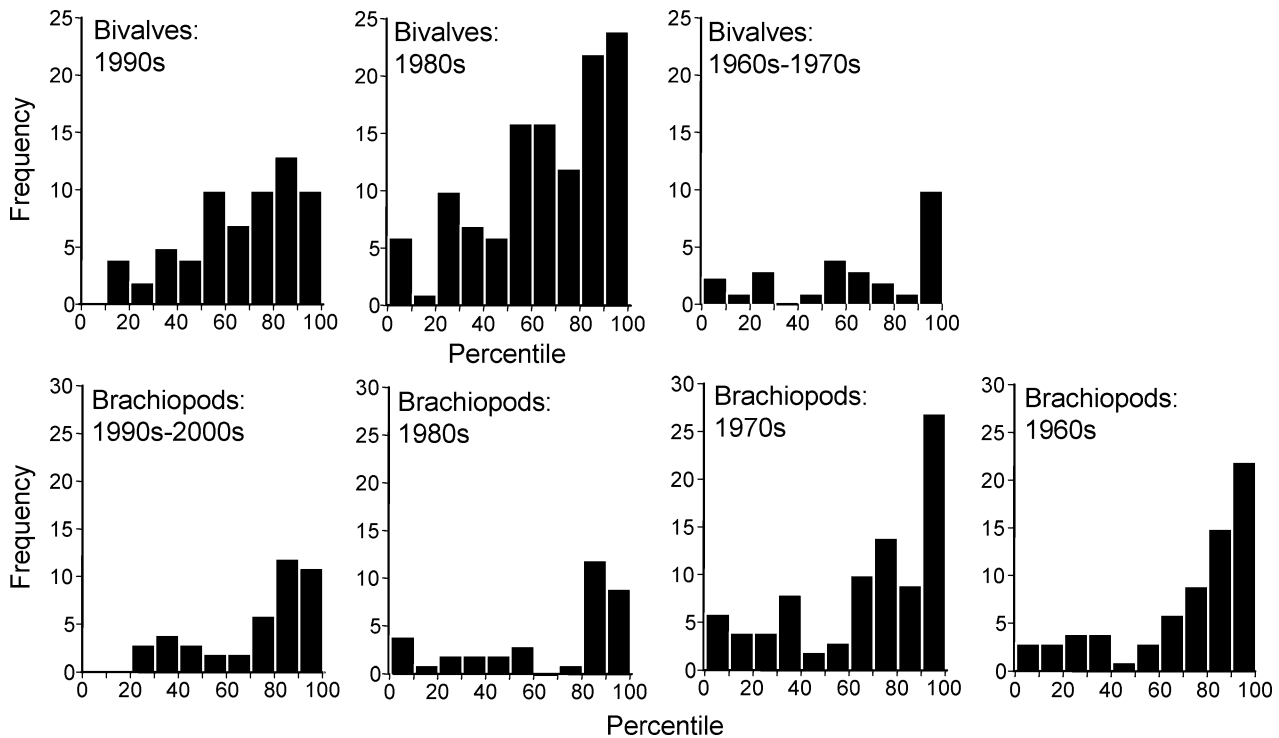

FIGURE 10—Percentile-frequency distributions for bivalves and brachiopods grouped by year of publication of monographs from which data was collected.
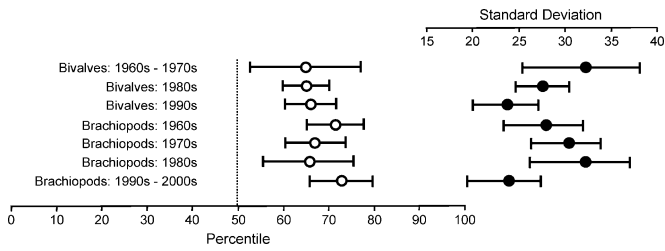
FIGURE 11—Means (open circles) and standard deviations (filled circles) of percentile-frequency distributions grouped by year of monograph publication. 95% confidence intervals computed with separate, 1000 iteration bootstrap simulations.

opposite in effect to the artificial fining of grains sizes in automated image analysis (Sime and Ferguson, 2003) could cause this bias. Although we are unable to conceive of such a factor, we leave this as an open question for future research.

A more satisfying explanation for this bias is that the unconscious tendencies of authors are exerting two opposing forces on these data. As mentioned earlier, 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. It is certainly true that the largest size classes (90th to 100th percentile) are the most oversampled group in terms of specimens imaged in monographs (Figs. 4, 7, 10, 13), but the other size classes above the 50th percentile have numerous representatives in the percentile-frequency distributions as well. Therefore, it is also possible that there is a second, perhaps weaker, tendency toward picking representative specimens in terms of the size distribution of the population. This tendency may cause authors to try to avoid the largest individuals when choosing specimens to figure because they are, by definition, aberrant in terms of their size. The interplay between these two tendencies may result in the bias that is illustrated here.

Effect of Indeterminate Growth

In this study, measurements on specimens in the bulk sample are considered a proxy for the underlying size distribution of the species. This is a common methodology but it is complicated by the fact that the organisms considered here, bivalves and brachiopods, have indeterminate growth. As a result, the average size in a population mostly reflects the

age structure and can change dramatically if, for example, juveniles are included in the analysis. Thus, the resulting distribution is always partly dependent upon the methodological choice of what size range to measure. This is why some macroevolutionary studies of size use maximum rather than mean size, despite the statistical difficulties presented by extreme values (Jablonski, 1997; Roy et al., 2000; Lockwood, 2005).

To partially circumvent this problem, monographs were not used if the authors explicitly stated that juveniles were included in the size distributions. Likewise, juvenile specimens that were figured were not included in the monograph sample for a species. In many of the monographs, however, these criteria were ineffective because the authors did not reveal if juveniles were included. In fact, most of the monographs did not give any details about sampling methodology with respect to specimen size range because the size distribution of a species was not the primary concern of these publications. Thus, the problem of indeterminate growth cannot be fully addressed in this meta-analysis, and the mean of the bulk sample may not always be an accurate predictor of the actual mean size of reproductive adults in a given population. It is, however, doubtful that this substantially changes the monographic bias in any one direction. More likely, any discrepancies between the actual population mean and the bulk sample mean for a species are negated when a large number of species with data from independent sources are considered.

Effect of Sample Size

While the potential confounding factors of geography and year of publication have little effect on the monograph bias, sample size does, in some cases, have a moderate effect on the pattern of bias. The plots shown in Figure 14 are similar to the funnel plots that characterize many meta-analyses (Palmer, 1999), in that the mean size in a species' bulk sample is estimated less precisely as sample size (both bulk and monograph) decreases. This funnel effect is probably inevitable, but researchers should be aware of it and make an effort to restrict their data so that it does not have a significant effect on the parameter of interest. For example, in this study bulk sample size was restricted to $n \geq 10$. This arbitrary and *a priori* decision was made so that size-frequency distributions with adequate sample size could be constructed for each species. The funnel shape in both plots of bulk sample size versus percent difference indicate that larger cut-off sample sizes could have been used to further reduce the variation in percent difference among species (Fig. 14), but this would reduce the number of species considered in the analysis.
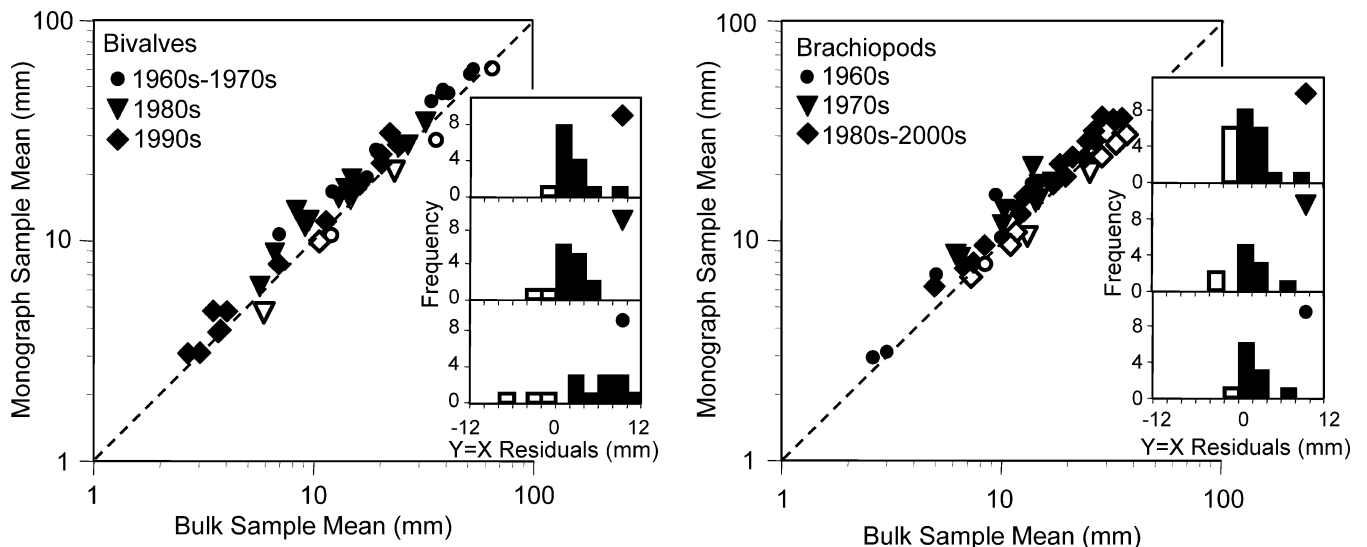

FIGURE 12—Scatter plots with least-squares regressions show results of species-level analysis with data grouped by year of monograph publication. Statistical parameters associated with these regressions given in Table 4. Inset plots show residuals computed from line of equality. Open symbols and white columns indicate monograph data biased in a negative direction with respect to the bulk sample.
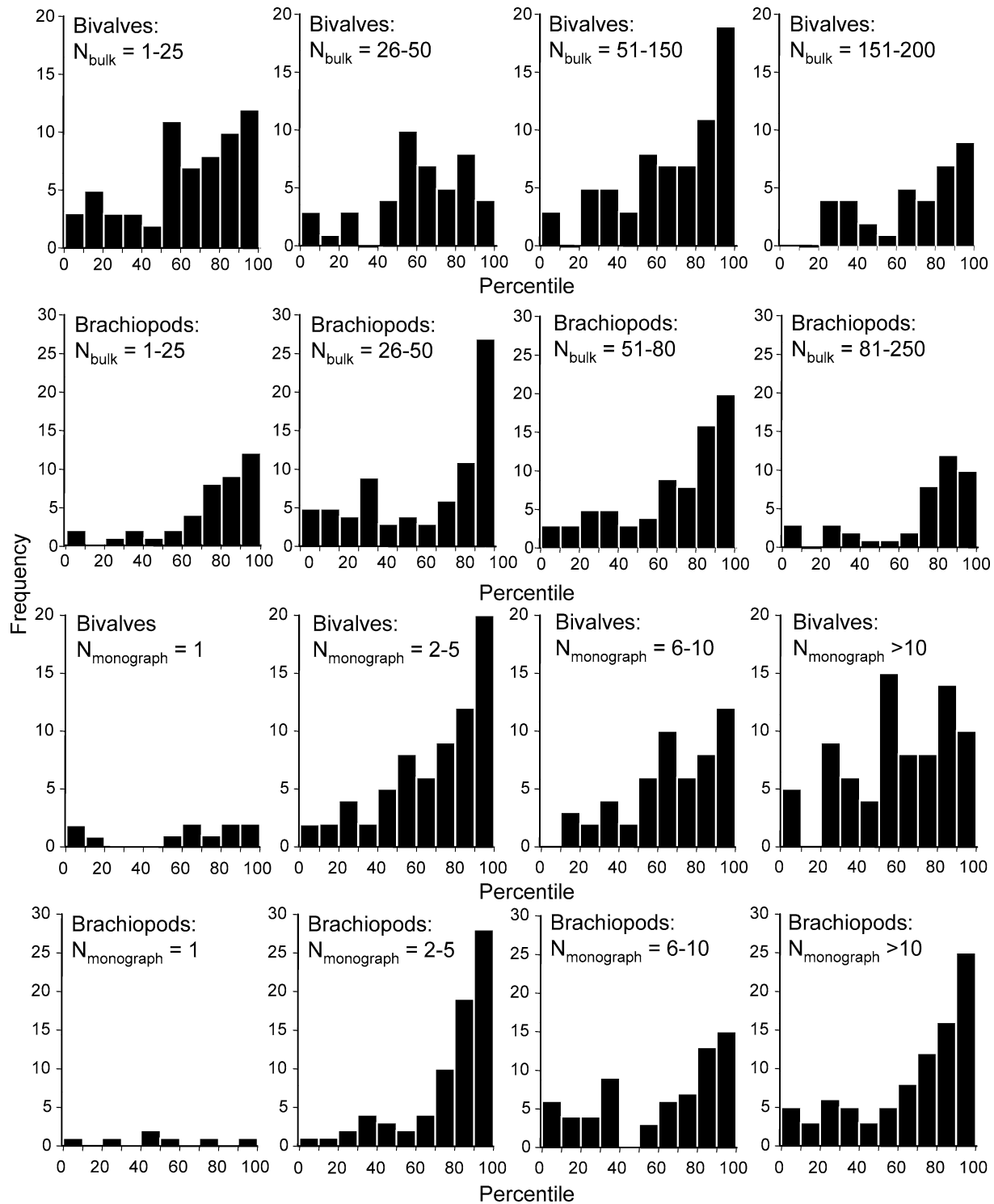
FIGURE 13—Percentile-frequency histograms with data grouped by bulk sample size (upper two rows) and monograph sample size (lower two rows) for each species.

The most important factor is that there is no significant correlation between bulk sample size and percent difference for either bivalves or brachiopods. Thus, the criterion of n ≥ 10 for bulk sample size worked well for this analysis and would probably be a good starting point for future analyses of this type.

The consideration of monograph sample size illustrates a somewhat different outcome. In the specimen-level analysis of sample size groups, the percentile distributions constructed for monograph sample size in brachiopods was the only group to show a significant difference among the distributions (Fig. 13; Table 5). This difference may, however, result from the large difference in sample size among these distributions. A more revealing look at how monograph sample size affects the monograph bias is given in the species-level analysis in Figure 14. In the two plots on the left side of Figure 14, the funnel effect (Palmer, 1999) can be seen, although it is much clearer for bivalves than it is for brachiopods. In fact, bivalves show no correlation between percent difference and monograph sample size, whereas brachiopods show a significant positive correlation between these two variables. Thus, as monograph sample size for bra-
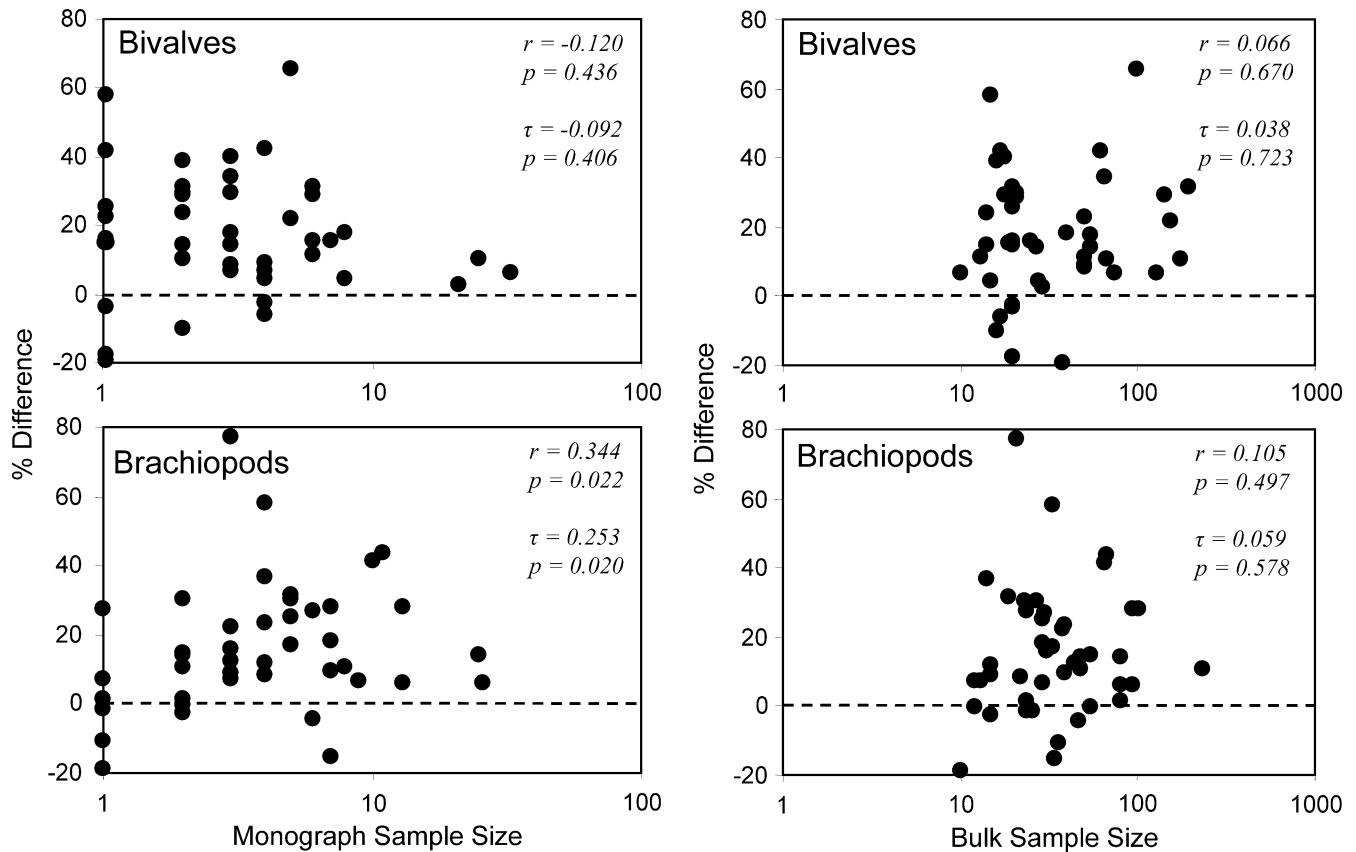
FIGURE 14—Percent difference between monograph and bulk sample means for each species, plotted against monograph sample size (plots on left) and bulk sample size (plots on right) for each species. See text for details on the calculation of differences. Dotted lines indicate no difference in mean size between the monograph and bulk sample for a species. Measures of association: r = Spearman's rank correlation; τ = Kendall's rank correlation; p = two-tailed probability.

chiopods increases, the monographic bias also increases. This pattern is mostly caused by the unexpected low variation in percent difference at low monograph sample size. It is unclear whether this represents an actual difference in the monographic bias between bivalves and brachiopods or if this is a sampling artifact. One indication of the latter is the fact that when monograph samples are restricted to $n > 1$, the correlation between monograph sample size and percent difference in brachiopods is insignificant ($r = 0.139$, $p = 0.413$; $\tau = 0.103$, $p = 0.390$). Clearly, this specific pattern needs further investigation. In future analyses it may be prudent to restrict image-based studies of body size to species with monograph sample sizes of 2 or greater.

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 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 15.

The monograph sample and the bulk sample for each species were compared by grouping bivalve and brachiopod data into epochs (Fig. 15). 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. 15). 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 15 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 15 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.

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
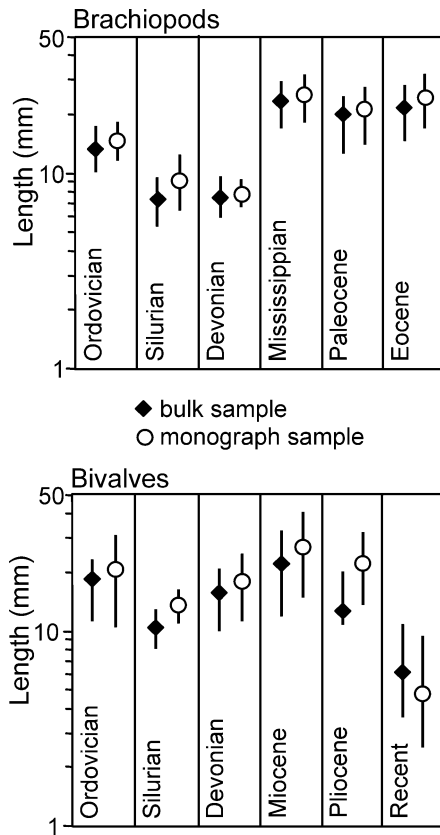
FIGURE 15—Comparison of the mean of species means from monograph and bulk sample for each epoch in dataset. 95% confidence intervals calculated with separate 1000 iteration bootstrap simulations. Sample sizes for each epoch are as follows. Brachiopods: Ordovician, 11 species; Silurian, 11 species; Devonian, 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.

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. Nevertheless, we do not advocate a change in taxonomic methodologies, as 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, as 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.

ACKNOWLEDGMENTS

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