Ecosystem-wide body-size trends in Cambrian–Devonian marine invertebrate lineages

Philip M. Novack-Gottshall

Abstract.—Fossil marine lineages are generally expected to exhibit long-term trends of increasing body size because of inherent fitness advantages or secular changes in environmental conditions. Because empirical documentation of this trend during the Paleozoic has been lacking for most taxonomic groups, the magnitude, timing, and taxonomic breadth of the trend have remained elusive. This study uses the largest existing database of fossil invertebrate sizes from four faunally important phyla to document ecosystem-wide size trends in well-preserved biotas from deep-subtidal, soft-substrate assemblages during the Cambrian through Devonian. Size of type specimens was measured along standard body axes from monographic plates and converted to body volume by using a broadly applicable empirical regression. Results demonstrate that mean body size (herein volume) of individual genera doubles during this interval, especially from the Late Ordovician through Early Devonian. The timing is gradual in spite of major radiations and extinctions, and the increase is primarily attributable to a net increase in the three-dimensionality of genera. The overall increase is not caused by replacement among clades because increases are widespread among arthropods, brachiopods, and echinoderms, at the phylum and class levels; in contrast, mollusks do not display a net size change at either taxonomic level. The increase is also more pronounced in microbivores than in carnivores. Combined with known environmental changes during this interval, and especially records of carbon dioxide, these trends provide support for the claim that primary productivity increased during the early to mid Paleozoic.

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Body size is one of the most frequently used phenotypic traits for documenting macroevolutionary trends (McNamara 1990) because it is measured easily and because it is correlated with a variety of ecologically and evolutionarily meaningful traits (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Cope's rule—the tendency for size to increase over time—is the most commonly studied size trend (Stanley 1973; Jablonski 1997; Gould 1988; Alroy 1998; Kingsolver and Pfennig 2004; Novack-Gottshall and Lanier 2008), but trends can also reflect episodic evolutionary or environmental changes (MacFadden 1986; Dommergues et al. 2002; Lockwood 2005; Payne 2005). Documentation of size trends in fossils has focused almost exclusively on Cenozoic and Mesozoic lineages (e.g., MacFadden 1986; McKinney 1990; Jablonski 1997; Alroy 1998; Dommergues et al. 2002; Finkel et al. 2005; Hunt and Roy 2006; Hone and Benton 2007). Despite widespread predictions of Paleozoic size increases related to increasing productivity and nutrient availability (Bambach 1993, 1999;

Vermeij 1995), quantitative documentation is limited to the following: three orders of Cambrian–Devonian trilobites (Trammer and Kaim 1997); Cambrian–Devonian brachiopods from a single habitat (Novack-Gottshall and Lanier 2008); Ordovician trilobites (Finnegan and Droser 2006), bivalves, and brachiopods (Krause et al. 2002; Stempien et al. 2005), and North American brachiopods (Payne and Finnegan 2006); and Permian (through mid-Triassic) gastropods (Payne 2005). Such temporally and taxonomically restricted studies hinder broader understanding of synoptic size changes during the Paleozoic. Given the centrality of body size as an indicator of important evolutionary and environmental changes, documenting a general Paleozoic size trend remains a vital goal (see Payne and Finnegan 2006). This paper uses the largest existing database of fossil invertebrate sizes to document size trends in four major marine phyla during the Cambrian through Devonian.

Interpretation of size trends is complicated,

unfortunately, because such trends can reflect causative evolutionary dynamics as well as artifacts of heterogeneous sampling along environmental gradients. For example, size has been shown to correlate with temperature, ocean chemistry, latitude, bathymetry, and food availability, among others (Smith et al. 1995; Rex et al. 1999; McClain and Rex 2001; Finkel et al. 2005; McClain et al. 2005; Hunt and Roy 2006). One solution to limiting such conflating factors is to restrict sampling to a single habitat (Bambach 1977). Here, size trends are documented from the deep-subtidal, soft-substrate habitat, a well-defined marine habitat renowned for its plentiful sedimentary record, excellent preservation of in situ fossil assemblages, and fairly homogeneous environmental conditions (Brett 1990; Schieber et al. 1998). Environmental heterogeneity was further controlled for bathymetry and oxygenation, the two environmental conditions most known to affect the size of benthic biotas (McClain and Rex 2001; Roy 2002; McClain et al. 2005).

Because of our poor understanding of size trends during the Paleozoic, several basic—but as yet unanswered—questions are addressed here. (1) Magnitude: What is the overall trend in size and its magnitude during this interval? Is the trend one of size increase, stasis, or decrease? Is the trend caused by driven (biased) or passive (unbiased) causes? (2) Timing: Are changes gradual or pulsed? How does size change during intervals of evolutionary diversification and mass extinction? Is the trend correlated with, and therefore potentially caused by, trends in environmental parameters? (3) Taxonomic breadth: To what extent are trends manifested in parallel or independently among separate phyla and classes? Do ecosystem-wide trends reflect the accumulation of trends within lineages, or replacement (sorting) among lineages?

Materials and Methods

Habitat Focus and Sampling.—To focus on macroevolutionary trends within one environmental setting, fossil collections were restricted to normally oxygenated, deep-subtidal, soft-substrate, open-shelf and fore-delta settings at or below storm wave base. Bathymetry was controlled by sampling only assemblages from fine-grained siliciclastic and carbonate mudstones and shales occasionally interbedded with thin limestones, siltstones, and calcisiltites; all collections lack calcareous algae and sedimentary structures indicative of shallow water (Holmes 1957; Jennette and Pryor 1993; O'Brien et al. 1994). Oxygenation was controlled by excluding collections indicating dysoxic and anoxic conditions, determined from biotic and sedimentological criteria (depauperate, low-oxygen-adapted biotas; abundance of pyrite/sulfides; thinly laminated strata lacking burrowing [Schovsbo 2001; Gaines and Droser 2003]). Such standardization is important here because oxygen-stressed conditions are typically associated with diminutive faunas (Cloud 1948). All such environmental assessments were made uniformly by this author, in most cases guided in part by evaluation of independently published studies and personal communication dealing with sequence stratigraphy, sedimentology, and geochemical studies. Variations in paleolatitude, geography, temperature, and seawater and sediment geochemistry were not addressed formally and could play confounding roles benefiting future analyses. Even though taphonomic preservation in such deep-subtidal settings is often exceptional (Brett and Allison 1998), I did not attempt to standardize collections taphonomically here (cf. Novack-Gottshall 2007) because taphonomic heterogeneity is not expected to affect the size of fossils in such settings. Similarly, collections were not standardized for size (in terms of either number of fossils or rock volume).

Taxonomic Coverage.—Collections with faunal lists surveying entire biotas were chosen preferentially. To focus on typical benthic fossils from this habitat, I discarded all putative nektonic and planktonic taxa and those of clearly exotic nature (e.g., Devonian sunken trees) were discarded from collections. Although there is some disagreement over the life habits of extinct cephalopods, members of this class were included here when analyses of taphonomy, environmental distribution, and functional morphology demonstrated they were nektobenthic or demersal members of benthic faunas (e.g., Frey 1989; Westermann

TABLE 1. Summary of total, phylum-level, and class-level databases used in analyses. The phylum-level database (also the overall database analyzed here) is the total database subset of occurrences of four phyla; the class-level database is the nested subset of occurrences of eight classes. Occurrences are the sum of all individual genus (or genus-equivalent) occurrences across all time bins; taxa occurring in more than one bin will have multiple occurrences. All other taxonomic totals are measures of total unique richness.

	Total	Phylum-level	Class-level
Occurrences	4380	3874	3505
Phyla	17	4	4
Classes	49	33	8
Genera	1260	1079	939
Species	2314	2027	1818

TABLE 2. Taxonomic resolution of size data in the phylum- and class-level databases. N is the number of genera (or genus equivalents) coded at a particular taxonomic level. Approximately half the taxa are coded at genus or finer level. Most taxa coded at higher taxonomic levels were indeterminate genera in recognizable families or orders (e.g., Bellerophontidae indet.) known from other occurrences in the database to display limited volumetric size variation (<1 base-ten log-unit); the size of such indeterminate taxa was estimated from the size of a contemporaneous (same geological period) type species in each indeterminate taxon.

	Phylum-level		Class-level	
	N	Cumulative %	N	Cumulative %
Species	145	13.4%	130	13.8%
Genus	380	48.7%	340	50.1%
Family	340	81.7%	317	85.5%
Order	80	97.8%	65	98.7%
Class	10	99.9%	0	100.0%

1999; Westermann and Tsujita 1999). To focus on typically preserved fossil taxa, I also discarded taxa with soft-part preservation, occasionally found in collections. Taxa for which body size estimates were unavailable or unable to be measured reliably were also discarded.

Database Characteristics.—The resulting database encompasses 4380 taxon occurrences in 322 collections from 114 published sources (Table 1), part of a larger database (Novack-Gottshall 2007) documenting the comparative paleoecology of Cambrian through Devonian, deep-subtidal, soft-substrate assemblages. Most collections were compiled from the global literature, with several collected in the field (e.g., Novack-Gottshall and Miller 2003). Collections were dated to stage-level resolution, and placed in bins representing approximately equal 11-Myr durations (mean = 11.4 Myr, standard deviation = 2.8 Myr) with boundary dates taken from Gradstein et al. (2004) and supplemented with correlations of the Paleobiology Database (accessed August 2006). The analyses here focus on size trends in four phyla combined (Arthropoda, Brachiopoda, Echinodermata, and Mollusca, hereafter termed the overall trend), in these four phyla separately, and in eight major constituent classes (Trilobita, Lingulata, Rhynchonellata, Strophomenata, Crinoidea, Bivalvia, Cephalopoda, and Gastropoda), taxa chosen because they are the most common and best studied members of Paleozoic biotas. Their size dynamics are probably representative of other

Paleozoic taxa because they encompass, in aggregate, more than 80% of the occurrences in the entire database (Table 1).

Size Measurement and Allometric Conversion to Volume.—Adult body sizes of database taxa were measured on illustrations in taxonomic monographs. Although such illustrations typically portray larger-than-average specimens (Kosnik et al. 2006; Krause et al. 2007), the bias is consistent across taxonomic groups, sizes, and geological time, and resulting patterns are meaningful so long as measurement sources are consistent internally, as is the case here. Anteroposterior, transverse, and dorsoventral (ATD) measurements were made with calipers, in millimeter units, on monograph illustrations following established protocols (Novack-Gottshall 2008). In total 42 monographs were used, chiefly volumes of the *Treatise on Invertebrate Paleontology* (Moore et al. 1953–2006). Taxonomic resolution was made to the lowest level possible (Table 2), supplemented with analog models of contemporaneous (i.e., from the same geological period), taxonomically related, and morphologically similar taxa. For example, when all three dimensions were not available for a taxon, such analogs were used to determine an appropriate isometric model to estimate non-illustrated lengths. Approximately half the taxa in the database were coded at genus or finer level (Table 2). Most taxa measured here at higher

levels were indeterminate genera in recognizable families or orders (e.g., Bellerophontidae indet.) known from taxa in the database measured at genus or species level to display limited size variation; higher taxa displaying large volumetric variation at a given geological period (greater than one base-ten log-unit) were not used in analyses. Analyses were conducted at the scale of genus (or genus-equivalent: a species of such an indeterminate higher taxon). Each genus was estimated from a congeneric species chosen at random. Substituting related taxa (i.e., congenerics or confamilials) has little effect on size measurement (Kosnik et al. 2006). Such approximations may affect variation in data but should not bias resulting trends, especially considering the range of sizes included here.

Because this analysis includes taxa with diverse morphologies, body volume was used as a common measure of body size. Body volume was estimated for each taxon by using the product of the three ATD measurements (in centimeter units): $\log_{10}$(volume, ml) $= 0.896$ $\log_{10}$(ATD, cm^3) $-$ 0.265 (Novack-Gottshall 2008: eq. 5). This equation is appropriate for use with a wide range of Paleozoic benthic invertebrates and is consistent with known morphological allometries of diverse taxa (McMahon 1973; Niklas 1994). Resulting volumetric estimates are inexact but unbiased estimates (accurate to within one base-ten log-unit) and appropriate given the wide range (in size, morphology, and taxonomy) of taxa included here. Although some taxa measured here (notably echinoderms) were not used in developing the equation, the apparent generality of the equation in predictive tests (Novack-Gottshall 2008), and especially the concordance of the equation dynamics with known morphological allometries of crinoids and other Paleozoic echinoderms (see Novack-Gottshall 2008), warrants extrapolating it cautiously with these taxa.

Time-Series and Maximum Likelihood Modeling of Size Evolution.—Size distributions were made by extracting all unique genera (or genus-equivalents) within each bin. Mean size and standard error within each bin were calculated from 2000 bootstrap replicates (with replacement) (Efron and Tibshirani 1993). If these distributions are skewed, trends in the mean and extremes (minima and maxima) can be sensitive to sample size. To assess this possibility, rarefaction (Sanders 1968; Hurlbert 1971), standardized at 40 genera per bin (with 2000 replicates), was conducted on overall trends in the mean and minimum. Size trends were analyzed for both the overall database aggregate and separately at two taxonomic scales (four phyla and eight classes) to evaluate the role of clade replacement (sorting) in producing the aggregate trend. Trends were also analyzed at two trophic levels (microbivores and carnivores sensu Novack-Gottshall 2007) to evaluate the role of productivity and nutrient availability in driving these trends. Trends in individual A, T, and D measurements were analyzed for the overall trend and among taxonomic subgroups to evaluate trends in these raw measurements, to assess reliability of the allometric equation for volume, and to characterize the generality of size trends among lineages.

Although ancestor-descendent comparisons within a phylogenetic context are ideally preferred for assessing trend mechanisms (Jablonski 1997; Alroy 2000; McShea 1994, 2000; Wang 2005), such comparisons are not feasible here. Trend mechanisms were therefore evaluated in three less powerful ways on the basis of changes in size distributions through time; such results are still insightful because they can validate the generality of size increase during the Paleozoic, regardless of its causes. The one-sided Mann-Whitney *U*-test was used to test whether overall mean size increases through geological time; two-sample bootstrap tests using standardized sample sizes (2000 replicates with 40, 90, and 140 genera per period) resulted in similar results and are not presented here. The second approach evaluates the behavior of the minimum to distinguish biased (directional, driven) dynamics from unbiased (passive) ones. One well-established consequence of driven dynamics is a corresponding increase in the minimum observed size of individual taxa (Stanley 1973; Gould 1988; McShea 1994), whereas minimum size will remain constant in passive systems constrained by a lower size boundary. The third, most powerful approach uses maxi-

mum likelihood (R library paleoTS [Hunt 2006a,b]) to estimate the parameters underlying the behavior of size for three models: general (biased, driven, directional) random walk (GRW), unbiased (passive) random walk (URW), and stasis.

Both directional and unbiased random walk models use the observed distributions of sizes through time (in millions of years) to estimate the normal distribution from which size changes are drawn, with a mean (hereafter termed a directionality parameter) corresponding to the tendency to change (in units $\log_{10}$ ml/Myr) and a variance parameter corresponding to the volatility of changes around this mean. In the case of a positively directional trend (one in which size is driven to increase over time), the GRW model distribution will have a positive directionality parameter; a negatively directional trend will have a correspondingly negative parameter. The URW model is a nested special case of the GRW model with only a variance parameter (the directionality parameter is set to zero); resulting trends can accumulate size changes over time, but the changes are unbiased because there is an equal probability of size increases and decreases, with the volatility of changes attributable only to variance. Like the GRW model, the stasis model also has a normal distribution with two parameters (mean and variance), but the distribution corresponds to the optimal estimated size distribution from which all samples are drawn, independent of time. Accordingly, this model is one of non-autocorrelated white noise in which no net change is expected (Sheets and Mitchell 2001; Hunt 2006a).
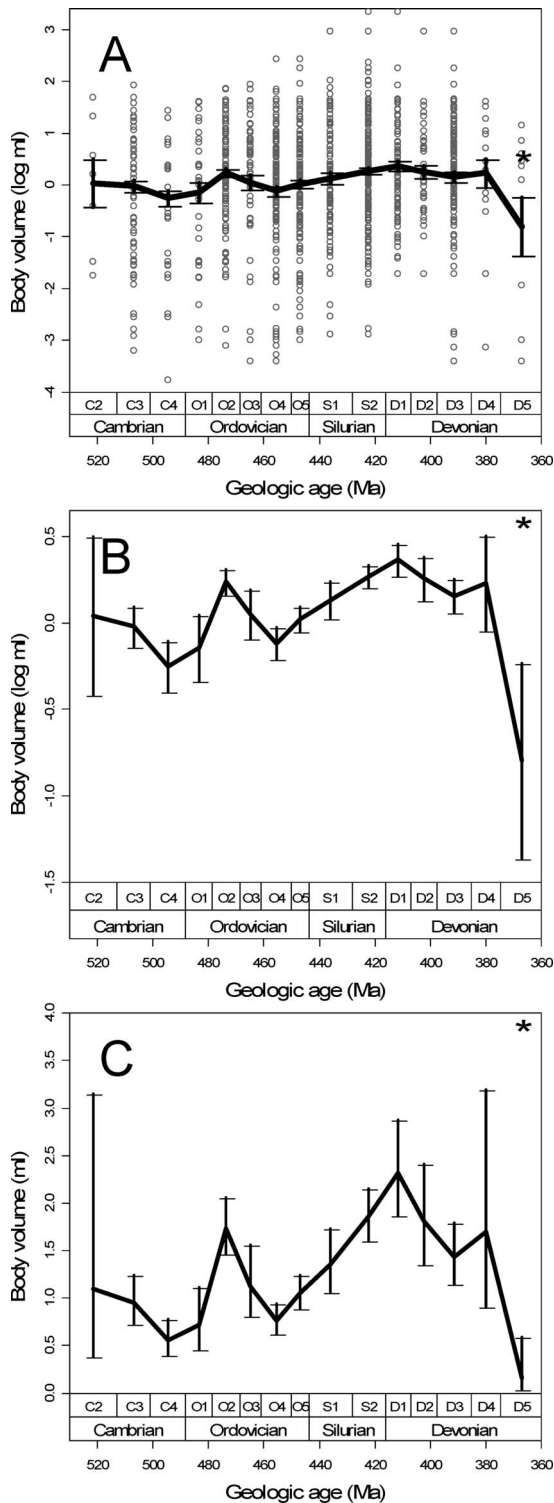
Each of these models also includes a normally distributed error term—estimated from the variance of observed sizes in each bin—incorporating the effects of sampling error (Hunt 2006a). The magnitude of such errors can affect the precision of resulting parameter estimates and the power of model selection because the observed distribution of data in a given interval will not correspond precisely to that interval's actual size distribution, which the models seek to estimate. Because sampling in most bins here is large and because there is significant heterogeneity in size variances among bins (see Hunt 2006a), these errors

were evaluated independently for each interval; that is, variance was not pooled among bins. These maximum likelihood models are robust to variations in number of intervals sampled and temporal spacing of samples (Hunt 2006a).

Models that are better supported by the data will have larger log-likelihood values than competing models. However, models with more parameters will benefit unfairly (that is, have a better fit) simply because of their greater complexity. When competing models have a similar model form (such as here), the small-sample unbiased Akaike Information Criterion (AIC_C) (Akaike 1974; Anderson et al. 2000) can be used to rank the fit of observed data to candidate models, with more complex ones penalized for their greater number of parameters. Better-supported models will have smaller AIC_C values. A simple way to compare the support for each model given the data is to use Akaike weights (Anderson et al. 2000), an approach that distributes model support across all candidate models so that the support for each model is expressed as a probability. In practice, overwhelmingly supported models have Akaike weights greater than 0.90, but alternative models with weights greater than 0.05 cannot be ruled out and might warrant additional scrutiny with additional data (Anderson et al. 2000; Johnson and Omland 2004). Such approaches to model selection have been used increasingly in evolutionary and ecological studies (e.g., Connolly and Miller 2002; Johnson and Omland 2004; Foote 2005; Hunt 2006a; Marcot and McShea 2007) because of their robust ability to evaluate multiple alternative hypotheses on equal footing simultaneously (Chamberlain 1890). All statistics and quantitative analyses used R 2.5.0 for Windows (R Development Core Team, 2007).

Results and Discussion

Magnitude and Timing.—Mean body size (measured as shell volume in milliliter units) of Paleozoic invertebrates (Arthropoda, Brachiopoda, Echinodermata, and Mollusca pooled) doubles gradually over 160 Myr of the lower and mid Paleozoic (Fig. 1). Although the overall trend is not monotonic at the resolu-

tion of series-level bins (Fig. 1B,C), mean size increases exponentially, incrementally, and significantly during each period, with mean volume of 0.74 milliliters during the Cambrian, 0.95 during the Ordovician, 1.30 during the Silurian, and 1.46 during the Devonian. The increase is gradual in that genera in younger, adjacent periods are not significantly larger (Table 3), but those in more distantly younger periods are; in other words, the size difference between periods increases (*p*-value decreases) consistently with temporal distance.

The overall mean trend is remarkable because of its gradualness in spite of significant evolutionary events during this interval, including the Ordovician radiation and two mass extinctions, at least at the coarse temporal resolution used here. The Cambrian radiation cannot be addressed because the C2 samples postdate this radiation (Bowring et al. 1993); overall size trends during this event have yet to be documented. Size remains quite stable, or perhaps decreases somewhat, during the mid through late Cambrian, increasing into the Ordovician. The Ordovician radiation, generally coincident in this habitat with the transition from Cambrian to Paleozoic Evolutionary Faunas (Sepkoski 1981; Sepkoski and Miller 1985; Peters 2004), does not appear to have affected mean size in a straightforward manner. An initial, substantial mean size increase during the late Early Ordovician (bin O2) is coincident with the onset of the radiation, but size decreases during the most extensive phase of the radiation during bin O4 (Webby et al. 2004). Gigantism has been claimed (e.g., Rohr et al. 1992; Jin 2001; Rud-

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FIGURE 1. Cambrian–Devonian trend in overall mean body volume of genera in deep-subtidal, soft-substrate assemblages. A, Trend showing individual genera (or genus equivalents), on logarithmic axis. B, Trend alone, on rescaled logarithmic axis. C, Trend alone, on linear axis. Asterisk is mean value during D5 bin when ostracodes are removed. Timescale is that of Gradstein et al. (2004), with 11-Myr bins used in Paleobiology Database. Each data point is the body volume for a single genus; many points overlap. Standard error bars around the mean are one standard deviation from the distribution of 2000 bootstrap replicates. Trend in median size, not shown, is nearly identical to mean trend.

TABLE 3. Mann-Whitney U-test comparisons on pooled sizes by period. One-sided tests compare whether genera in younger period are significantly larger than those in older period. p-values in bold note that genera in younger period are significantly larger than in older period. In all cases, genera in adjacent (younger and older) periods are not significantly larger (although the mean size increases through time), but those in subsequently younger periods are. Similar outcomes occur (not shown) when using two-sample bootstrap test after standardizing for differences in sample size (40, 90, and 190 genera per period) between periods.

	Cambrian		Ordovician		Silurian	
	U	p-value	U	p-value	U	p-value
Ordovician	72075.0	0.111				
Silurian	45177.5	**0.019**	173087.5	0.114		
Devonian	32874.5	**0.008**	125519.0	**0.036**	86045.5	0.254

kin et al. 2003) as a general feature of Late Ordovician (bin O5) biotas from Laurentian equatorial carbonates; although this shallow habitat is not represented here, mean size also increases in these deeper settings during this interval. Size continues to increase monotonically across the Late Ordovician mass extinction (O5/S1 boundary) and throughout the Silurian–Early Devonian (D1), stabilizing somewhat during remaining intervals. Sampling during the Late Devonian (D5) is insufficient to make a generalization about the effect of the Late Devonian mass extinction (D4/D5 boundary). An overall decline across this extinction is possible given the loss of many large-sized mid-Devonian clades (including extinction of all but three trilobite families and all atrypid and pentamerid brachiopods [Feist 1992; Hallam and Wignall 1997]); the decline here is the result of an abundance of D5 ostracodes. Bin D5 mean size without ostracodes (illustrated with an asterisk in Fig. 1) is 0.585 $\log_{10}$ ml, strongly consistent with an increasing Devonian trend.

The gradual but protracted nature of this overall trend is borne out in a maximum likelihood comparison of the models (Table 4). Al-though the unbiased (passive) random walk (URW) is the most strongly supported model, the directional (general, biased, driven) random walk (GRW) and stasis models have substantial support and cannot be ruled out currently as plausible alternatives. The low sensitivity of model selection results from the wide range of sizes in each bin (modeled here as large sampling error), in essence decreasing statistical power. Removing the poorly sampled, high-variance bins does not alter these results significantly, although combined support for the random walk models (GRW and URW) increases at the expense of the stasis model (combined Akaike weight equals 0.861 after removing bin D5, 0.934 after removing bins C2 and D5). The maximum likelihood estimate for the alternative GRW model directionality parameter ($\mu_{\text{step-GRW}}$, in units $\log_{10}$ ml/Myr) is consistent with the conclusion that a bias toward increasing size, if present, is positive and very close to zero; indeed, the GRW model has the highest log-likelihood value of all three models. If the GRW directionality parameter is truly small and close to zero, the URW model (with an assumed $\mu_{\text{step-URW}}$ value of zero [Hunt 2006a]) will near-

TABLE 4. Results of maximum likelihood comparison of evolutionary models for pooled occurrences of four Cambrian–Devonian phyla. ℓ is log-likelihood for the GRW, URW, and stasis models (Hunt 2006a), K is the number of parameters in each model, AIC_C is the small-sample unbiased Akaike Information Criterion. Unit for GRW and URW parameters is $\log_{10}$ ml/Myr; unit for stasis model is $\log_{10}$ ml. Relative model support is provided as a probability using Akaike weights; model weights with substantial (>0.05) support are highlighted in bold. Variance was not pooled across bins because of significant variance heterogeneity. Variance parameter values listed as zero here are very small ($p < 0.000000001$), but not precisely zero.

Model	ℓ	K	Parameters	AIC_C	Akaike weights
GRW	2.55	2	$\mu_{\text{step}}=0.003$, $\sigma^2_{\text{step}}=0.000$	-0.01	**0.199**
URW	2.32	1	$\sigma^2_{\text{step}}=0.000$	-2.31	**0.628**
Stasis	2.41	2	$\theta=0.101$, $\omega=0.176$	0.26	**0.173**

ly always have greater Akaike support because of its reduced number of parameters (Hunt 2006a) and because the nested relationship of the models prevents the URW model from having a higher likelihood value than the GRW. In other words, the URW model will nearly always win out over a weakly driven GRW model, even if the GRW model is the true model.

Sample-Standardized Trends in Mean and Minimum Size.—It is possible that the Paleozoic trend of increasing overall body size is an artifact of sampling heterogeneities among bins (Miller and Foote 1996; Alroy et al. 2001). Because the mean is sensitive to outliers and because larger genera are more likely to be encountered in more thoroughly sampled intervals, a trend of increasing size might be caused by more thorough sampling in younger bins (Stanley 1973; Gould 1988). This is not the case here. The overall relationship between genus richness and mean body size across bins is positive, but statistically not significant (linear regression: $r^2 = 0.192$, $p = 0.103$); the relationships within each period (excluding the two Silurian bins where such regressions are uninformative) are also not significant (p-values range 0.192–0.719). The positive relationship likely reflects an artifact of simultaneously increasing size and global species richness trends; there are more genera in the mid Paleozoic than during the early Paleozoic (Sepkoski 1997). Nevertheless, sampling was standardized at 40 genera per bin using rarefaction (Sanders 1968; Hurlbert 1971); standardization at 90 genera resulted in similar results, but included fewer intervals. As expected, the resulting trend (Fig. 2) is essentially unchanged from the raw trend (Fig. 1), demonstrating no clear effect of sampling heterogeneity on the increasing trend of size in Paleozoic invertebrates.

A general increase in the minimum trend (dashed line in Fig. 2) after rarefaction to 40 genera is also ruled out as an artifact of sampling heterogeneities. This increase is consistent with a driven cause to the mean trend (Stanley 1973; Gould 1988; McShea 1994), especially during the O4–D2 interval. This increase is unlikely to be driven by mid-Paleozoic biases in sampling against small taxa be-
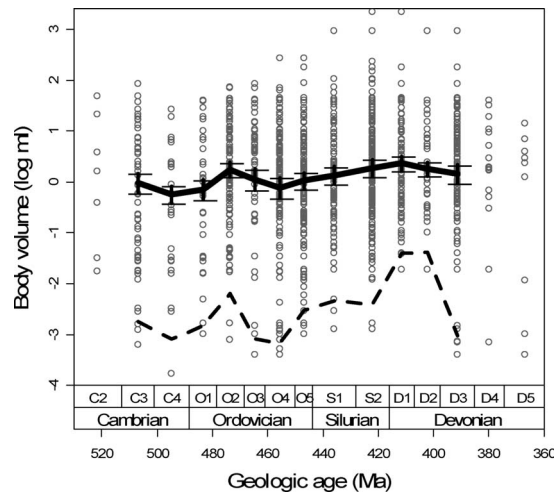

FIGURE 2. Sample-standardized, Cambrian–Devonian trend in mean and minimum body volume of genera. Trends are mean of 2000 bootstrap replicate samples of 40 genera (or genus-equivalents). Data points are the raw distribution of genus body volumes, as in Figure 1A. There were too few genera during the C2 and D4-5 bins to yield standardized estimates. Plot details are the same as in Figure 1A. Similar results (not shown) are observed when standardized to 90 genera per bin.

cause of the effort to locate samples encompassing whole biotas (see ''Materials and Methods''). Combined with the statistical results above, the overall size trend is consistent, therefore, with an overall weak but positive bias in size through time producing a significant net increase in mean size.

Assessment of Trends in Individual Size Lengths.—It is possible that the allometric conversion to volume obscures important trends in body size. This is addressed both by evaluating trends in the individual ATD measurements used to estimate volume in these genera graphically (Fig. 3) and by using maximum likelihood (Table 5). These results demonstrate that the Cambrian–Devonian doubling in mean volumetric size is caused primarily by a corresponding doubling in the net dorsoventral depth of taxa (Fig. 3C), by either a directional (GRW) or unbiased (URW) mechanism. There is no net change in anteroposterior length or transverse width, with both measurements sharing overwhelming support from the stasis model. In other words, the typical early and mid-Paleozoic invertebrate in this habitat, regardless of age, has a mean length and width of 21.3 mm and 14.6 mm re-
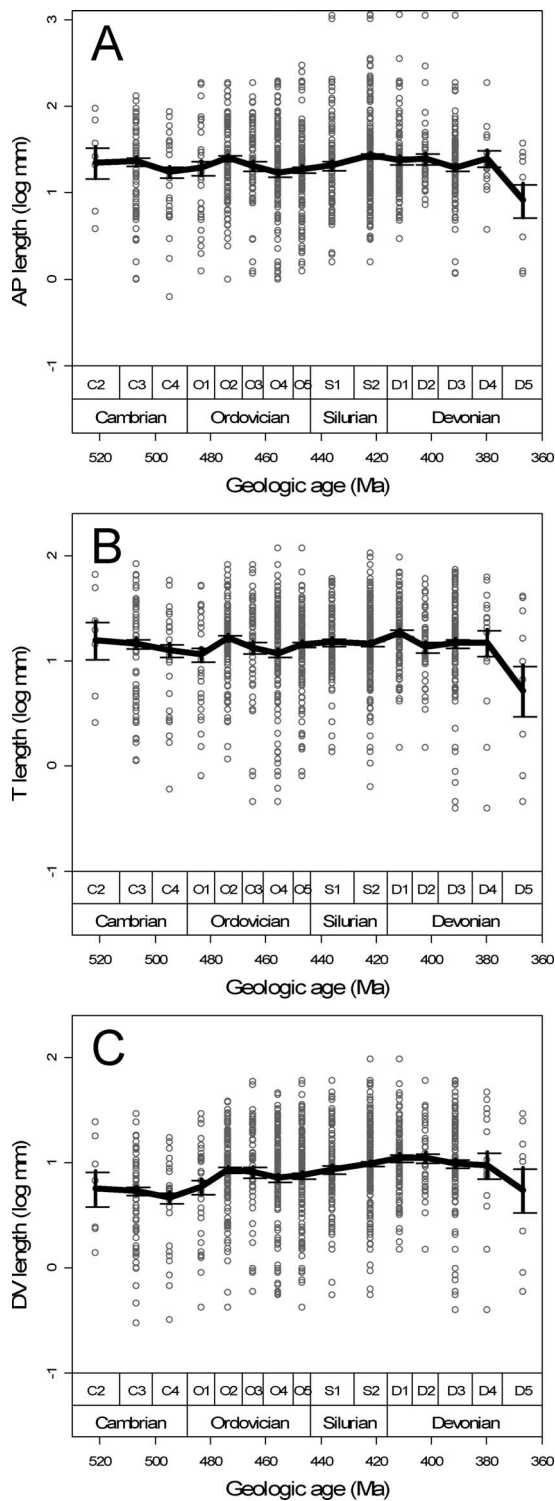
FIGURE 3. Individual Cambrian–Devonian trends in anteroposterior (A), transverse (B), and dorsoventral (C) body lengths. Plot details are the same as in Figure 1.

spectively, but depth increases from a Cambrian mean of 5.23 mm to a Devonian mean of 10.3 mm.

Similar ATD dimensional dynamics, however, are not consistent among the phyla and classes included here (Table 6). The magnitude and directionality of these ATD trends can be evaluated across taxonomic groups by focusing only on the maximum likelihood estimate of the directionality parameter for the GRW model, even though this model is not universally the best supported. The magnitudes of this parameter and the maximally supported models are generally similar for all three measures within each group. Thus, the overall volumetric trends must result, at least in part, from replacement of clades of differing geometric morphology through time. Because the three measurements are multiplied together when estimating body volume here (see Novack-Gottshall 2008), it is a simple task to evaluate the relative contribution of each length to the overall volumetric trend. In other words, the maximum likelihood estimate of the directionality parameter for volume is equal to the sum of directionality parameters for ATD lengths within each taxonomic group (and as evident by comparing these values in Tables 6 and 7). Although full discussion of these relationships is beyond the scope of this paper, it is relevant to point out that the contribution of the directionality parameter for dorsoventral depth is the most positively directed parameter for all taxonomic groups, except the gastropods (where transverse width has the largest value) and lingulatans and echinoderms (where anteroposterior length has the largest value). The number of instances of dorsoventral depth having the largest value is significant using the chi-square test ($\chi^2 = 9.5$, d.f. = 2, p-value = 0.009). Thus, even though broadly similar trends are displayed across measurements within most taxonomic groups, proportionally greater increases in dorsoventral depth account for a taxonomically widespread component of these overall trends.

This increasing three-dimensionality of early and mid-Paleozoic invertebrates has been hypothesized previously (Thomas et al. 2000). Mid-Cambrian invertebrates from the Burgess

TABLE 5. Results of maximum likelihood comparison of random walk models for trends in anteroposterior, transverse, and dorsoventral body lengths for four pooled Cambrian–Devonian phyla. Details are the same as in Table 4. Variances within each group were not pooled across bins because of significant variance heterogeneity.

Length	Parameters					AIC_C			Akaike weights		
	$\mu_{step\text{-}GRW}$	$\sigma^2_{step\text{-}GRW}$	$\sigma^2_{step\text{-}URW}$	θ_{stasis}	ω_{stasis}	GRW	URW	Stasis	GRW	URW	Stasis
Anteroposterior											
(A)	0.000	0.000	0.000	1.329	0.003	−17.23	−19.97	−25.12	0.018	**0.070**	**0.913**
Transverse (T)	0.000	0.000	0.000	1.164	0.001	−18.66	−21.49	−29.90	0.004	0.015	**0.982**
Dorsoventral											
(D)	0.002	0.000	0.000	0.906	0.011	−29.43	−30.57	−14.89	**0.361**	**0.639**	0.000

Shale (correlative with bin C3 here) disproportionately were found to utilize simple rods and external supports to achieve larger skeletal sizes; skeletons (especially internal and remodeled skeletons) better suited for larger size and more complexly integrated morphologies did not evolve until later. Taken together, these results demonstrate significant morphological changes in Paleozoic invertebrates. They also caution against relying solely on single morphological measurements to characterize important trends in body size.

Phylum- and Class-Level Taxonomic Breadth.—Such a long-term increase in ecosystem-wide body size can result from pooled size increases across many taxonomic groups or from replacement among groups, with larger groups succeeding smaller ones. These alternatives are addressed by examining size trends both among the major benthic groups from this habitat and at two taxonomically nested scales of four phyla and eight classes.

Despite an increase in mean size during the Late Ordovician through Early Devonian, the size trend in arthropods (primarily trilobites and ostracodes) (Fig. 4) is best supported by a weakly negatively directional or unbiased random walk model (Table 7). This result is attributed primarily to the considerable number of small ostracodes in these Late Devonian (D5) collections; removing this bin results in strongest support for the stasis model (Akaike weight = 0.542) but with some support for a weak, positively directional model ($\mu_{step\text{-}GRW}$ = 0.0007 with Akaike weight = 0.086). A long-term increase, coincident with increasing minimum size, is well exhibited in the trilobites (Fig. 5) alone, with strong support for unbiased, or alternatively directional, random walk dynamics. It might be argued that this

TABLE 6. Maximum likelihood estimates for directionality parameter for trends in individual size measurements for various groups during the Cambrian–Devonian. Values of directionality parameter, μ_{step}, from GRW model, with 95% confidence intervals. −0.000 denotes that parameter estimate is negligibly negative. Bold denotes that GRW model is the best supported model; italics denote that stasis model is the best supported; asterisk denotes that model is overwhelming supported (>0.90) using Akaike weight. Variances within each group were not pooled across bins because of significant variance heterogeneity.

Group	Anteroposterior	Transverse	Dorsoventral
Phylum:			
Arthropoda	−0.006 (±0.006)	−0.006 (±0.006)	−0.002 (±0.004)
Brachiopoda	**0.004 (±0.002)***	**0.005 (±0.002)***	**0.006 (±0.002)**
Echinodermata	*0.005 (±0.010)*	*0.002 (±0.006)*￼*	*0.004 (±0.007)*
Mollusca	*0.001 (±0.004)**	−0.000 (±0.004)	*0.002 (±0.003)*
Class:			
Trilobita	0.000 (±0.003)	0.001 (±0.003)	0.003 (±0.003)
Lingulata	*0.004 (±0.007)*	*0.002 (±0.005)*	*0.001 (±0.005)**
Rhynchonellata	0.003 (±0.002)	0.003 (±0.002)	**0.004 (±0.002)**
Strophomenata	0.002 (±0.003)	0.001 (±0.003)	*0.004 (±0.006)*
Crinoidea	−0.002 (±0.010)*	−0.001 (±0.011)	−0.001 (±0.011)
Bivalvia	*0.001 (±0.004)**	*0.001 (±0.004)**	0.002 (±0.004)
Cephalopoda	−0.003 (±0.005)	−0.000 (±0.003)	*0.001 (±0.002)**
Gastropoda	*0.003 (±0.006)*	*0.005 (±0.008)**	*0.003 (±0.006)**

TABLE 7. Results of maximum likelihood comparison of evolutionary models for various groups during the Cambrian–Devonian. N and Bins are the number of genus occurrences and the number of time intervals included in each analysis, respectively; remaining details are the same as Table 4. Variances within each group were not pooled across bins because of significant variance heterogeneity.

| Group	N	Bins	Parameters					AIC_C			Akaike weights		
			$\mu_{step\text{-}GRW}$	$\sigma^2_{step\text{-}GRW}$	$\sigma^2_{step\text{-}URW}$	θ_{stasis}	ω_{stasis}	GRW	URW	Stasis	GRW	URW	Stasis
Phylum:													
Arthropoda	539	14	−0.013	0.024	0.024	−0.022	0.800	31.62	29.53	40.97	**0.260**	**0.737**	0.002
Brachiopoda	574	15	0.013	0.000	0.001	−0.268	0.245	−1.90	3.03	29.34	**0.922**	0.078	0.000
Echinodermata	154	11	0.009	0.022	0.023	0.844	0.090	25.99	23.04	18.83	0.024	0.106	**0.870**
Mollusca	277	14	0.003	0.000	0.000	0.403	0.000	9.56	6.86	−4.00	0.001	0.004	**0.995**
Class:													
Trilobita	482	13	0.004	0.002	0.002	0.478	0.068	9.53	6.88	13.47	**0.204**	**0.768**	0.028
Lingulata	60	12	0.007	0.000	0.000	−0.594	0.000	22.92	20.04	16.78	0.037	0.158	**0.805**
Rhynchonellata	354	14	0.010	0.000	0.000	−0.038	0.035	2.33	2.57	16.22	**0.530**	**0.470**	0.001
Strophomenata	163	11	0.006	0.004	0.004	−0.029	0.099	18.05	15.22	16.79	0.143	**0.588**	0.269
Crinoidea	85	9	−0.006	0.042	0.043	1.287	0.135	28.12	24.43	20.58	0.020	0.125	**0.855**
Bivalvia	121	12	0.004	0.000	0.000	0.269	0.000	8.79	5.92	2.10	0.030	0.125	**0.845**
Cephalopoda	42	12	−0.001	0.000	0.000	1.602	0.000	3.09	0.06	−2.21	**0.051**	0.231	**0.718**
Gastropoda	80	10	0.011	0.011	0.012	0.535	0.033	20.69	17.65	12.18	0.013	0.060	**0.927**
Diet:													
Microbivores	1211	15	0.007	0.000	0.001	−0.128	0.046	6.93	6.33	9.09	**0.372**	**0.502**	0.126
Carnivores	385	15	−0.014	0.067	0.068	0.514	0.361	46.09	43.70	37.78	0.015	0.049	**0.937**
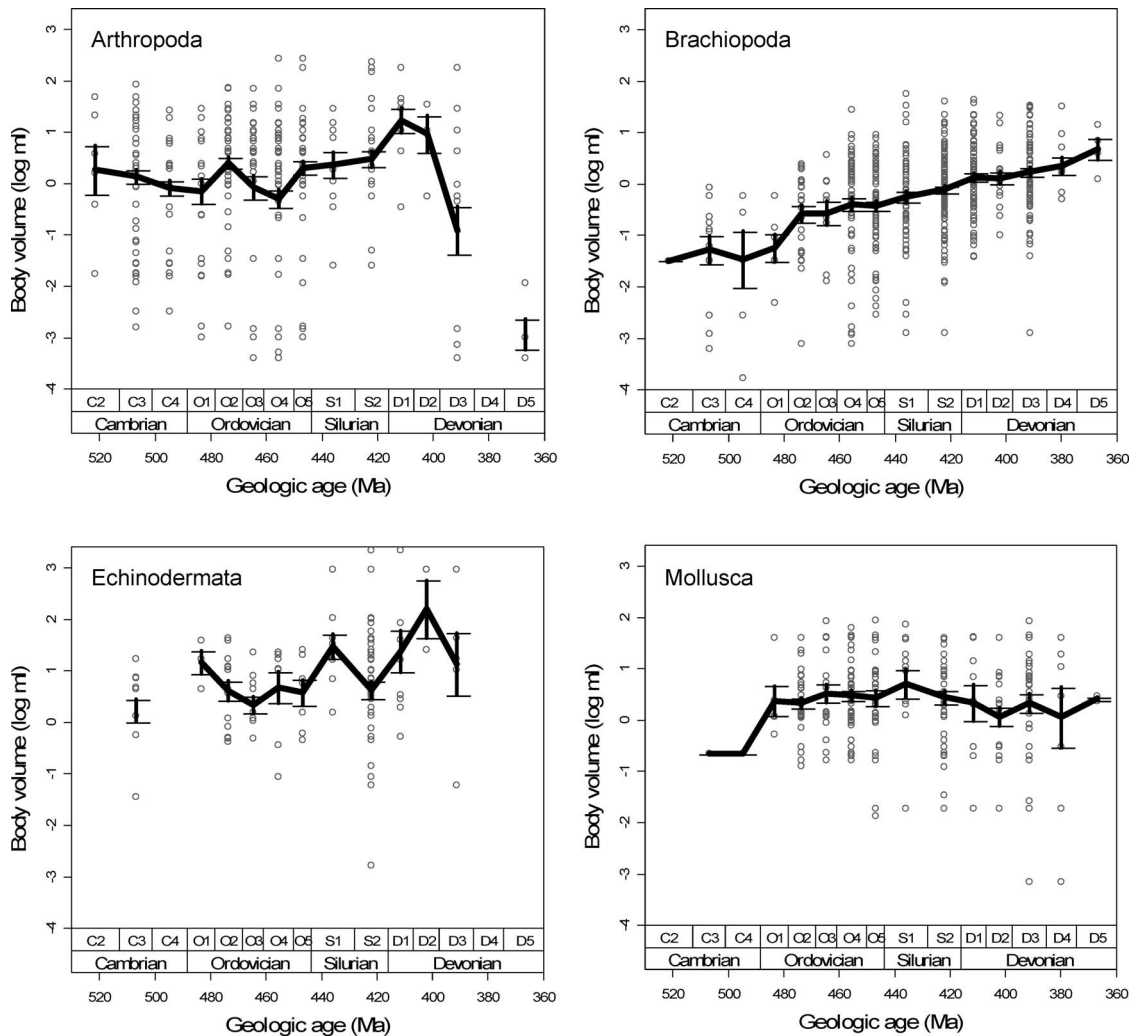
FIGURE 4. Cambrian–Devonian trends in mean body volume of four common phyla in deep-subtidal, soft-substrate assemblages. Plot details are the same as in Figure 1.

increase is caused by the extinction of small agnostid trilobites in the Ordovician. However, miniaturization was taxonomically widespread and quite common in non-agnostid trilobites during the Cambrian and Ordovician (Fortey and Owens 1990); there are 21 occurrences of such trilobites here, including the smallest trilobite in the database, *Shumardia pusilla*, with estimated volume of 0.0016 ml (using measurements from Harrington et al. 1959:O245). This overall increase is consistent with those in other studies (Trammer and Kaim 1997; Churchill-Dixon 2001; Finnegan and Droser 2006), although the present study

encompasses a much longer period of time and broader taxonomic coverage.

The brachiopods (Fig. 4), including three classes (Fig. 5), display a striking Cambrian–Devonian increase in mean and minimum size. This greatly extends the Ordovician trends noted in other studies (Jin 2001; Stempien et al. 2005; Payne and Finnegan 2006; Harper et al. 2006). Brachiopods as a whole and the rhynchonellatans are best fit by the GRW model (Table 7) with a weak positive tendency, although all trends have substantial support for URW. The increase in the lingulatans occurs primarily during the Early Pa-
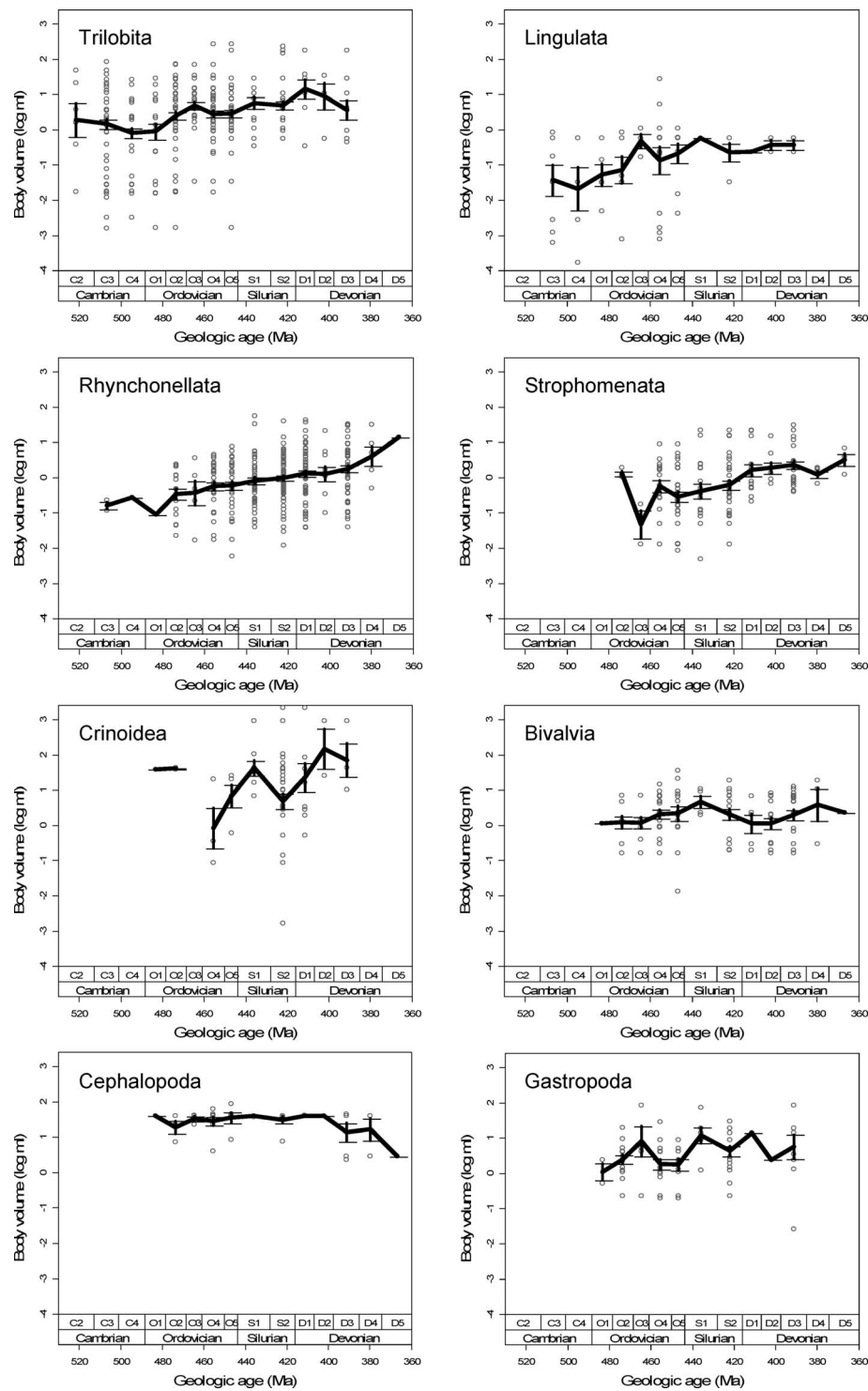
FIGURE 5. Cambrian–Devonian trends in mean body volume of eight common classes in deep-subtidal, soft-substrate assemblages. Plot details are the same as in Figure 1.

leozoic, with stability during the mid Paleozoic. Although URW cannot be ruled out, this trend is best supported by stasis. Like the trilobites, it is not the result of the extinction of a small-sized clade; the smallest lingulatans, Order Acrotretida, also display size increases here through the Silurian (Novack-Gottshall and Lanier 2008). In fact, increasing size dynamics consistent with Cope's rule are observed in nearly all long-ranging brachiopod orders in these data. However, the increase is not manifested within familial lineages; the tendency for size increase occurs primarily during the initial origination of individual families (Novack-Gottshall and Lanier 2008).

The echinoderms (Fig. 4), including the crinoids (Fig. 5), have variable but generally increasing patterns, with size increases most pronounced in the Late Ordovician through Devonian. Although there is some support for URW (Table 7), the wide range of sizes makes it impossible to rule out stasis as the best model for both taxonomic levels. Overwhelming support for stasis occurs in the mollusks (Table 7, Figs. 4, 5), with no net increase observed at the phylum or class levels. In fact, cephalopods may display a weakly negative tendency during just the Devonian. Shorter-term dynamics are consistent with a previously claimed trend of size increase in Ordovician bivalves (Stempien et al. 2005). Although these two phyla and four classes have fewer genus occurrences than the previous two phyla, their greater support by the stasis model is unlikely to be an artifact of reduced sampling for several reasons. AIC$_C$ includes a bias-correction factor that accounts for differences in both the length of time series (number of bins) and the number of model parameters. Hunt (2006a) demonstrated that model selection is reliable for time series with as few as five bins—sampling thresholds that are well surpassed here (Table 7). Like the directional GRW model, the stasis model (with two parameters) also requires substantially better support to have greater Akaike weight than the URW model (with one parameter). Thus, the switch away from a directional trend in these taxonomic groups is likely a genuine signal.

Despite much variation in timing and magnitude among groups, most Paleozoic phyla and classes exhibit long-term increases in body size, especially during the Late Ordovician through Early Devonian. These across-taxonomic-group increases are generally observed individually in ATD lengths (Table 6), with a greater increase generally in dorsoventral depth. Although most trends are consistent with URW dynamics based on Akaike weight (Table 7), the data are insufficiently powerful to rule out additional models in most cases. The mollusks, and possibly echinoderms, are best supported by stasis models and the brachiopods (and within them the rhynchonellatans) are substantially supported by directional models.

Interpreting Shared Causes

The average genus within deep-subtidal, soft-substrate habitats doubles in size during the Cambrian through Devonian. This increase is taxonomically widespread, affecting arthropods, brachiopods, and possibly echinoderms at the phylum and class level; mollusks notably do not exhibit any long-term change in size. Although it is not possible at present to determine unambiguously whether the overall increase is caused by directional or unbiased dynamics, this increase is gradual, prolonged, and impervious to major evolutionary radiations, extinctions, and biotic turnovers, at least given the temporal resolution here.

Such taxonomically and morphologically widespread dynamics among members of the same Ordovician–Devonian ecosystem are strong evidence for a common cause. Such a shared cause is significantly bolstered because these groups share little in terms of their morphological traits, ecological life habits, or phylogenetic relationships, and because the increases are manifested primarily in dorsoventral thickening. Because collections were standardized for major environmental and sampling heterogeneities, it is unlikely that the trends are an artifact of sampling. The simplest remaining explanation is a long-term change in the environmental conditions in this ecosystem.

Comparison of the overall size trend with records of Cambrian–Devonian environmental conditions rules out several causes. Recon-

structed atmospheric oxygen dynamics (Berner 2006) do not resemble these size trends. Paleozoic sea-level changes are also unlikely because they peak in the Late Ordovician (e.g., Haq and Al-Qahtani 2005; Miller et al. 2005) rather than in the Devonian, as does size here. A potential negative relationship exists for atmospheric carbon dioxide concentration based on recent geochemical modeling (Berner 2004, 2006; Royer et al. 2004; Royer 2006; but not Rothman 2002). Both trends display generally monotonic changes (size increasing, carbon dioxide decreasing) starting in the Cambrian, undergoing coincident minor reversals during the Early Ordovician, continuing through much of the Devonian before reversing again in the Late Devonian. Carbon dioxide has been much used (Berner 2004; Royer et al. 2004; Royer 2006; Came et al. 2007) as a proxy for sea-surface temperature, which is itself associated with body size in marine taxa (Finkel et al. 2005; Hunt and Roy 2006). Given this conflation of factors, it may prove difficult to distinguish whether the primary forcing agent here is temperature or carbon dioxide. It may be notable that a pH-corrected $\delta^{18}O$ paleotemperature record (Vezier et al. 2000 modified in Royer et al. 2004, and see Came et al. 2007) does not appear to match the present size trend during the Ordovician and Silurian. In any case, this relationship should remain preliminary pending statistical analyses using higher-resolution time-series data.

Such a relationship between size and climate warming, however, is compelling because it long has been implicated in the Phanerozoic history of biodiversity (Vermeij 1987, 1995; Bambach 1993, 1999; Martin 1996, 2003; Payne and Finnegan 2006). Vermeij (1995), in particular, hypothesized that concomitant increases in carbon dioxide, temperature, and sea level during periods of pervasive submarine volcanism and oceanic rifting significantly promoted primary productivity and nutrient availability. Bambach (1993, 1999) made similar claims, with additional emphasis on the attendant effects of terrestrialization on marine ecosystems, especially during the Ordovician–Devonian. Both predicted that such ecosystem-wide changes would facilitate the diversification of more abundant and stable

populations, more intensive competitive interactions, more energetic and efficient metabolisms and activities, and the potential for adaptive innovations. An additional prediction—one linked directly with these other consequences—was an increase in the body size of organisms. Given the ''superoligotrophic'' marine conditions during the Paleozoic (sensu Martin 1996) and the combination of tectonic, oceanographic, and climatic conditions required by the Vermeij and Bambach scenarios, it stands to reason that body size may be a first-order indicator of Paleozoic ecosystem productivity (see Payne and Finnegan 2006).

This hypothesis—that increased Paleozoic primary productivity promoted ecosystem-wide size increases—is tested here by comparing size trends in organisms grouped according to dietary trophic levels (microbivores and carnivores) reliably inferred in the fossil record. Microbivores (see Novack-Gottshall 2007) are low-level consumers that feed on bacteria, protists, and algae and include many deposit and suspension feeders, among other foraging habits. This functional group here is taxonomically diverse, including 28 classes in these four phyla, dominated, in descending order, by various rhynchonellatans, trilobites, strophomenatans, bivalves, crinoids, gastropods, and lingulatans that collectively account for 86% of microbivore occurrences. Carnivores are high-level consumers that feed on other animals; this functional group here includes nine classes, dominated by various trilobites, ostracodes, and cephalopods that collectively account for 95% of carnivore occurrences. The large number of taxonomic groups in each group minimizes the role of phylogenetic biases.

Consistent with this productivity hypothesis, microbivores display a significant positive increase in body size throughout the Cambrian–Devonian (Fig. 6A), especially from the Late Ordovician through Early Devonian. The increase is well supported by both random walk models (Table 7), although the model of stasis cannot be ruled out. This is not simply an artifact of size increase in microbivorous brachiopods; the combined Akaike support for random walk models remains essentially
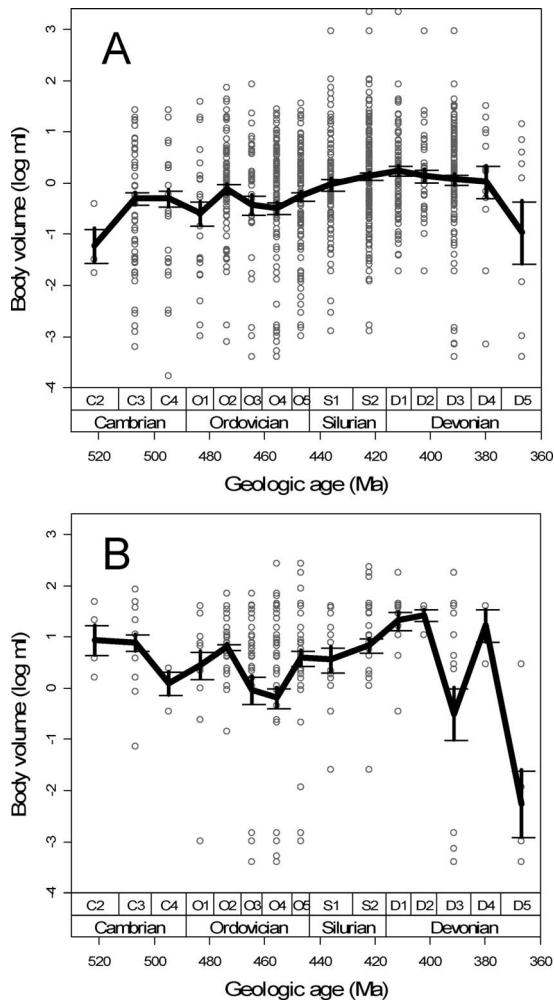
FIGURE 6. Cambrian–Devonian trends in mean body volume of microbivores (A) and carnivores (B) in deep-subtidal, soft-substrate assemblages. Plot details are the same as in Figure 1.

unchanged, 0.860, when brachiopods are excluded. In contrast, carnivores (Fig. 6B) are dynamically variable, with a possible decrease during the Cambrian-Ordovician followed by a comparable increase through the Early Devonian; this net constant size is overwhelmingly supported by the stasis model (Table 7). The timing of the mid-Paleozoic increases is coincident with the microbivorous trend, however, implying that both trophic groups experienced a common environmental driver, with lower trophic levels affected more so than higher levels. Although the trends are not parallel, carnivores significantly are larger than microbivores (one-sided t-test: $t = 6.484$,

$p < 0.0001$; one-sided Mann-Whitney U-test: $U = 321462$, $p < 0.0001$), as expected generally (Peters 1983). These trends, combined with the taxonomically widespread nature of increases and their association with a dorsoventral thickening among constituent taxa (Table 6), provide strong support for the hypothesis that size increase was driven by secular increases in productivity or nutrient availability during the Paleozoic, especially in deep-subtidal habitats during the Late Ordovician through Early Devonian.

It might be argued that the timing of these increases (and those in the various taxonomic groups above) lags behind the initial establishment of the environmental conditions necessary to promote such size increases. For example, Vermeij (1995) noted that the prerequisite environmental conditions necessary to enhance productivity and nutrient availability were set well before the mid Ordovician, a time when size here is mostly stable, instead of the Late Ordovician, when size here begins to increase. Two explanations may reconcile this lag. First, the Cambrian size stability might be indicative of different biotic reactions to these conditions by the Cambrian versus Paleozoic Evolutionary Faunas (Sepkoski 1981). Such an explanation might also explain why mollusks, members of the Modern Evolutionary Fauna, are exceptions to the other size increases reported here. Alternatively, or in combination, the lag may reflect a delay in the transfer of productive conditions from shallower, more coastal habitats to this deeper-water habitat (Bambach 1993).

Even if synoptic environmental changes played an important role in causing or facilitating this increase, this documentation does not explain how, in a mechanistic sense, size actually increased. For example, it remains unanswered whether the environmental changes simply set in place a necessary precondition for size to increase by ecological or evolutionary mechanisms, whether the environmental changes drove the size changes directly, or whether some other mechanism was at work. For the brachiopods at least, Novack-Gottshall and Lanier (2008) noted that size increase was manifested primarily by a positive size bias in the origination of brachiopod fam-

ilies, with no relationship thereafter between mean familial body size and the longevity or genus richness of these families.

The comparison of size trends among phylogenetically and ecologically unrelated taxa living in the same habitat is an important and powerful test of such ecosystem-level processes because environmental changes will often affect entire communities of organisms in a similar manner. Such analyses also have the benefit of being less prone to sampling artifacts (Bambach 1977). This comparative ecological perspective can contribute significantly to our understanding of past environmental changes, while offering a broader context for understanding within-lineage analyses.

Acknowledgments

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