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Body size, energetics, and the Ordovician restructuring of marine ecosystems

Seth Finnegan and Mary L. Droser

Abstract.—Major shifts in ecological dominance are one of the most conspicuous but poorly understood features of the fossil record. Here we examine one of the most prominent such shifts, the Ordovician shift from trilobite to brachiopod dominance of benthic ecosystems. Using an integrated database of high-resolution paleoecological samples and body size data, we show that while the average local richness and relative abundance of trilobites declined significantly through the Ordovician, the estimated standing biomass of trilobites, and by implication the amount of energy that they used, remained relatively invariant. This is attributable to an increase in the average body size of trilobite species in our data set, and especially to the widespread occurrence of the exceptionally large Middle–Late Ordovician trilobite genus *Isotelus*. Brachiopods increase in both mean body size and relative abundance throughout the Ordovician, so that estimates of brachiopod biomass and energetic use increase substantially between the Early and Late Ordovician. Although the data set includes a range of depositional environments, similar trends are observed in both shallow subtidal and deep subtidal settings. These results suggest that diversification of the Paleozoic Fauna did not come at the energetic expense of the Cambrian Fauna. The declining relative abundance of trilobites may reflect a combination of numerical dilution and the necessary energetic trade-offs between body size and abundance.

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Introduction

One of the most remarkable episodes of biodiversification in Earth history took place during the Ordovician Period (490–443 Ma). Numerous clades experienced major evolutionary radiations during this interval, increasing global diversity of marine genera by more than 300% (Sepkoski 2002). These radiations dramatically changed the structure of marine ecosystems as benthic paleocommunities dominated by trilobites and other members of the Cambrian Evolutionary Fauna (EF) gave way to paleocommunities dominated by rhynchonelliform (articulate) brachiopods and other members of the Paleozoic EF (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Peters 2004), establishing an ecological regime that persisted broadly for the remainder of the Paleozoic Era.

The nature of this restructuring is controversial. Although it is clear that the *relative* species richness and abundance of trilobites, the principal members of the Cambrian EF, declined in nearshore and midshelf environments, it is not clear whether this indicates true decline in their ecological significance or is simply due to passive numerical dilution by the expanding Paleozoic EF (Westrop and Adrain 1998a,b; Westrop et al. 1995). The ecological implications of these two interpretations are quite distinct. The first implies either that there were competitive interactions, direct or diffuse, between the Cambrian and Paleozoic EFs (Sepkoski and Miller 1985; Sepkoski and Sheehan 1983), or that the shift in dominance reflects physical transitions in benthic environments that favored the Paleozoic EF over the Cambrian EF (e.g., Miller and Connolly 2001). The second scenario instead implies that the Paleozoic EF diversified and became taxonomically dominant by radiating into comparatively open ecospace (Valentine 1973), taking advantage of resources that were underutilized by the Cambrian EF (Bambach 1983, 1985).

This distinction between actively and passively driven shifts in dominance lies at the heart of many questions about major ecological transitions in the fossil record (Gould and Calloway 1980; Benton 1996, 1997; Sepkoski

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1996; Miller 1998; Sepkoski and Miller 1998; Vermeij 2004). Competitive interactions, whether direct or indirect, are fundamentally about the distribution of energy and nutrients, but shifts in dominance have usually been examined using global-scale species or genus richness data. This approach has been criticized both because it is unclear how short-term, local ecological interactions scale up to generate global macroevolutionary patterns (Dietl and Vermeij 2006), and because it implicitly assumes that all species are ecologically equivalent when it is clear from study of modern ecosystems (Brown 1995; Kerr and Dickie 2001) that this is never true.

In recognition of these limitations, recent analyses have begun to incorporate abundance data as well (Wing et al. 1993; Lupia et al. 1999; Sepkoski et al. 2000; Novack-Gottshall and Miller 2003; Peters 2004, 2006; Finnegan and Droser 2005; Bush et al. 2007). However, abundance by itself is an incomplete measure of ecological significance, if ecological significance is understood to have a specifically *energetic* connotation (Bambach 1993; Vermeij 2004). Another critical factor, which is rarely considered in paleoecological studies, is body size.

Because mass and per-individual metabolic rate increase with body size, while population density tends to decrease with body size, standing biomass (average body mass $\cdot$ abundance $\cdot$ area^{-1} $\cdot$ time^{-1}) and population energetic use (energy$\cdot$area$^{-1}\cdot$time^{-1}) are not predictable on the basis of abundance alone (Damuth 1981, 1987a; Blackburn and Gaston 1997). This relationship, termed the Energetic Equivalence Rule (Damuth 1981) invalidates abundance as a metric of biomass or energy use when, as is normally the case, the species under consideration span a wide range of body sizes. It also makes the prediction that, all else being equal, increases in mean body size, often observed in the fossil record, should be accompanied by decreases in abundance. Hence, understanding the ecological context of major faunal transitions in the fossil record requires integrating abundance and body size data.

Here we combine a database of high-resolution paleoecological samples with a database of trilobite and rhynchonelliform brachiopod body sizes to estimate Ordovician trends in biomass and energy use for these two ecologically and taxonomically important groups. We show that due to substantial increases in the average body size of both trilobites and brachiopods in our data set between the Early and the Late Ordovician, these trends differ significantly from trends in genus richness and relative abundance, and have markedly different implications for the nature of ecosystem restructuring during the Ordovician biodiversifications.

Data and Methods

Samples.—Our data set includes 357 fossil collections from the Ordovician of the United States (see Supplementary Table 1 online at http://dx.doi.org/10.1666/07074.s1) that meet the following criteria:

1. Collected from units representing shallow to deep subtidal (above storm wave base) mixed carbonate-clastic depositional environments.
2. High stratigraphic resolution (single bed or small group of beds).
3. Counts of all shelly macrofaunal elements reported, all trilobites and rhynchonelliform brachiopods identified at least to genus, minimum sample size of 20 individuals (median = 61, mean = 78, max = 554).
4. Good preservation quality (original shell calcite in most brachiopod and trilobite taxa).

The database contains extensive collections from the type areas of each of the four stratigraphic series of the Ordovician System in North America: our own Ibexian (Lower Ordovician) and Whiterockian (Middle Ordovician) collections from Utah and Nevada, and published data sets from the type Mohawkian (lower Upper Ordovician) in New York (Titus 1986; Titus and Cameron 1976) and the type Cincinnatian (upper Upper Ordovician) in Kentucky and Ohio (Holland and Patzkowsky 2004). Additional published data sets are included from the Ibexian of central New York (Westrop et al. 1993) and the Mohawkian–Cincinnatian of western Virginia (Springer 1982) and Tennessee (Patzkowsky and Holland

1999). Although the Lower-Middle Ordovician strata of the western United States and the Upper Ordovician strata of the eastern United States represent different tectonic settings, both were at tropical to subtropical latitudes throughout the Ordovician and both represent mixed carbonate-clastic ramp and platform depositional settings (Brett et al. 2004; Ross et al. 1989). Moreover, data sets from these regions have been the basis for many previous studies of Ordovician paleoecological trends in North America, and have figured particularly prominently in studies suggesting that the ecological significance of trilobites declined through the Ordovician (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Miller et al. 1998; Peters 2004; Finnegan and Droser 2005).

The following temporal bins were used, based primarily on the timescale of Ross and Ross (1995): Ibexian 1 (Skullrockian–Tulean, 489.0–476.5 Ma), Ibexian 2 (Blackhillsian, 476.5–472 Ma), Whiterockian 1 (zone L of Ross et al. 1997, 472–470 Ma), Whiterockian 2 (zones M–O of Ross et al. 1997, 470–460.5 Ma), Mohawkian 1 (Ashbyan–Rocklandian, 460.5–454.5 Ma), Mohawkian 2 (Kirkfieldian–Shermanian, 454.5–451 Ma), Cincinnatian 1 (Edenian, 451–448.5 Ma), and Cincinnatian 2 (Richmondian–Maysvillian, 448.5–444 Ma).

Abundance.—For our Lower and Middle Ordovician collections, we calculated abundance as the minimum number of individuals of each genus present in each collection, following the protocols outlined by Gilinsky and Bennington (1994). Minimum numbers of individuals were also reported in most of the Upper Ordovician collections that we compiled from the literature; in the few cases for which no information on counting method was given, we assumed that that the reported counts represented minimum numbers of individuals. Determining minimum numbers of individuals is relatively straightforward for brachiopods, as they produce only two skeletal elements and all skeletal elements represent a dead individual. However, it is more difficult for trilobites. Trilobites produce multiple skeletal elements, but only some of these (the cephalon and sometimes the pygidium) are typically counted by workers seeking to estimate the minimum number of individuals. Thus, it is possible that trilobites are somewhat underreported in many collections relative to brachiopods. This may particularly be the case for species of the exceptionally large Middle–Late Ordovician genus *Isotelus* (see below for further discussion), which is often represented by highly fragmented shell elements. On the other hand, because trilobites grew by periodic molting, a given trilobite individual could produce multiple shell elements throughout its lifetime. Hence, the relative abundance of trilobite skeletal material in death assemblages may be inflated compared to the relative abundance of trilobite individuals in the communities from which they derive (following previous workers, we make the simplifying assumption that on average all trilobite individuals produced an equal number of molts over their lifetime). These complications make it difficult to directly evaluate the abundance of trilobite individuals in any collection, but if they apply uniformly to all collections in the data set then overall trends in the abundance of skeletal elements should be a reasonable proxy for trends in the number of individuals.

Population density (abundance with respect to area or volume) is the most energetically meaningful measure of abundance, but such data are almost never available for fossil collections and are subject to severe taphonomic limitations. We therefore use relative abundance as a proxy for population density. In calculating relative abundance we included all commonly reported shelly macrofauna (trilobites, articulate and inarticulate brachiopods, mollusks, echinoderms, bryozoans, and rugose corals, plus various minor groups). We excluded ostracods because of their small size, often extremely high abundance, and inconsistent reporting in faunal lists. Relative abundances were normalized for all figures using the standard logit transform for proportional data.

Because it is measured with respect to the number of individuals sampled, any analysis of trends in relative abundance must implicitly assume that total population density—the combined number of individuals belonging to all groups of interest—is constant through the sampled interval (Finnegan and Droser 2005). Given the great increase in diversity of benthic animals during the Ordovician Period, this assumption is very likely invalid in this case. Even if the absolute abundance of trilobites were invariant through the Ordovician, an increase in the total density of *all* benthic animals would have the effect of lowering the relative abundance of trilobites through numerical dilution (Westrop and Adrain 1998a; Westrop et al. 1995). Therefore, the relative abundance of trilobites in our Middle and especially Late Ordovician samples should be regarded as a minimum estimate of trilobite abundance. Although data normalization may likewise distort the abundance trajectory of brachiopods somewhat, there is universal agreement that the average population density of brachiopods increased dramatically during the Ordovician (Harper et al. 2004b).

Body Size.—Body volume estimates were based on measurements of brachiopod pedicle valves and trilobite holaspid cranidia. For Lower and Middle Ordovician species, we measured specimens from our own samples directly. Body sizes of Late Ordovician species were determined primarily from measurements of specimens in the collections of the Museum of Comparative Zoology, Harvard University. Whenever possible we measured specimens from the formations from which samples in our database derive, but in the few cases in which such specimens were not available we substituted conspecific or congeneric specimens from other units; excluding them has little effect on observed trends. Two species (*Bellefontia gyracantha* and *Clelandia parabola*) from the Ibexian tribes Hill Formation were measured from figured specimens published by Westrop et al. (1993). The number of specimens measured per species varied from one to 34, depending on availability, with a median of five for trilobites and nine for brachiopods. We made a special effort to measure multiple specimens of larger species, because the range of body volumes is far greater than in smaller species. The resulting averages are necessarily approximations, but given the five-order-of-magnitude variation in average body size in our data set it is highly unlikely that this overwhelms the underlying trend.

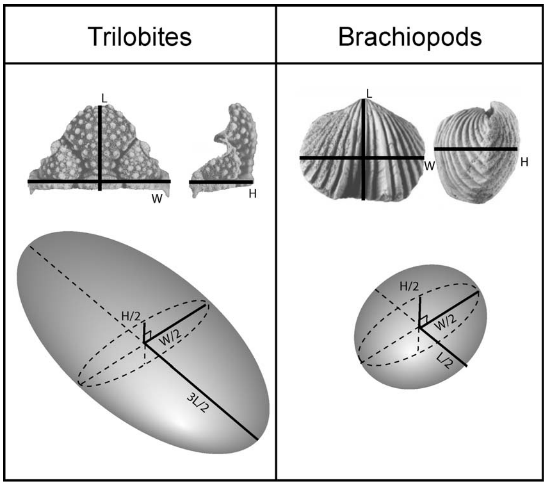

FIGURE 1. Measurements taken on trilobite and brachiopod specimens, and illustrations of the biovolume ellipsoids constructed from those measurements. For brachiopods, the ellipsoid radii were calculated by halving the length, width, and height measurements. Width and height radii were calculated in the same manner for trilobites, but because the length of the cephalon is only a fraction of the length of an articulated individual, the radius of the length dimension was determined by multiplying the length of the cephalon by a constant (see text) and dividing by two.

It is common and often sufficient to use a single length measurement as a proxy for body size in analyses of evolutionary size trends, but it is important to have three-dimensional information for estimating individual biomass and energy use (EU), because of the cubic scaling of body volume with size. Multiplying anteroposterior length, transverse length, and dorsoventral length (hereafter referred to as length, width, and height, respectively) captures most of the variation in biovolume across larges size ranges (Novack-Gottshall 2008b); here we use a slightly different approach, based on the same measurements, to model biovolume as an ellipsoid rather than a rectangular prism.

For brachiopods, length and width measurements on the pedicle valve, and the height of the articulated shell, were used to generate ellipsoids (Fig. 1) with a volume given by

$$(4/3)\pi(l/2)(h/2)(w/2), \qquad (1)$$

where l is the maximum length, w is the maximum width, and h the maximum height of the articulated skeleton. In cases in which articulated specimens could not be measured, we measured length and width on the pedicle valve and estimated height by using a height: width ratio generalized for different shell forms (concavo-convex, plano-convex, biconvex, or strongly biconvex). It should be noted that this approach overestimates biovolume, because it assumes that the thickness of the shell itself is negligible and that the internal volume of the shell is entirely filled with soft tissues. In fact, brachiopod shells can be quite thick, especially in inflated forms, and much of the internal volume of the shell is empty space. As long as the ratio of soft tissue to empty space is not size dependent, this does not introduce a systematic bias. An alternative approach, calculating biovolume simply as $l \cdot w \cdot h$, where h is not measured but is assumed to be constant across all sizes, results in changes in the size ranking of some taxa (Supplementary Fig. 1A, online at http://dx.doi.org/10.1666/07074.s2) but gives very similar estimates of biomass and EU trends (Supplementary Fig. 1B,C).

For trilobites, cephalon length, width, and height parameters were used to generate ellipsoids (Fig. 1). If the entire cranidium was available, measurements were based on it. The length of the whole organism was estimated as a multiple of the cranidium length, with different multipliers used depending on overall shape (i.e., long and thin versus short and broad). Similarly, when the height of the cephalon could not be accurately measured, height was estimated based on the degree of convexity (for example, a height:width ratio of 1:3 was used for the relatively inflated ''Illaeniform'' species, whereas a ratio of 1:6 was used for relatively flattened ''Oleniform'' species, and intermediate ratios for species falling between these end-members). Using a more generalized approach that assumes the same relative dimensions for all trilobites does not substantively change our results. As with the brachiopods, our approach overestimates biovolume, because the soft tissues of trilobites were generally concentrated in the axial lobe and the thin walking legs (Bambach 1993), with much of the remaining space enclosed by the exoskeleton relatively empty. We make the simplifying assumption that the ratio of soft tissue biomass to empty space was broadly similar in trilobites of all sizes. Although there is certainly considerable uncertainty in the size estimates derived from our geometrical approximations, even a factor of two or three error is minor compared to the multiple order-of-magnitude variation in body size exhibited by both trilobites and brachiopods in our data set.

Average body size was calculated as the arithmetic average volume of all individuals for each species. Average body size rather than median body size is the appropriate metric for this study, because large individuals account for biomass and energy use out of proportion to their abundance. In the rare cases in which no specimens of a species could be measured, that species was assigned the mean body size for other species in the same class and time bin. All of these species are numerically rare, and excluding them rather than assigning the average value has very little effect on observed trends.

Biomass.—We estimate biomass from relative abundance and body size. The biomass of a taxon within a sample is determined simply by multiplying its average body volume (we assume a linear relationship between body volume and body mass) by its relative abundance:

$$\text{Biomass} = nm \tag{2}$$

where m is the *average* body size of individuals in the population and n is the relative abundance of the species in the collection. We sum biomass estimates for all taxa in the sample to produce an estimate of the total relative biomass of each group represented in the sample.

Energy Use.—Whereas biomass is a relatively straightforward function of abundance and body mass, the energy required to sustain a population at equilibrium is a function of abundance and individual metabolic rate. Metabolic rates are affected by physiological and behavioral attributes that cannot be measured in fossil organisms, and are also influenced by ambient temperature (Gillooly et al. 2001). For members of the same clade inhabiting the same environment, however, these variables can largely be factored out. Within groups as ecologically and physiologically disparate as plants, mammals, fish, aquatic invertebrates, and protists, individual resting metabolic rate has been shown to scale as approximately the ¾ power of body mass (Gillooly 2001; Banavar et al. 2002). A recently developed general model uses this scaling relationship and biochemical kinetics to predict metabolic rate as a function of body size and ambient temperature (Gillooly 2001). This model has the form:

$$B(M,\ T) = B_0 e^{-E/kT} M^{3/4} \tag{3}$$

where B is individual resting metabolic rate, E is the average activation energy of rate-limiting biochemical metabolic reactions, k is Boltzmann's constant, T is absolute temperature, M is individual body mass, and B_0 is a taxon-dependent normalization constant. Because it varies only at high taxonomic levels, this constant can be factored out for estimating within-clade trends. Thus, a relative estimate of the *population* energy use (EU), the aggregate metabolic rate of individuals in the population (Savage 2004), is given by:

$$\mathrm{EU}(m,\ T) \propto e^{-1/kT} n m^{3/4} \tag{4}$$

Because all samples come from tropical to subtropical latitudes and relatively shallow water, we initially assume constant temperature (temperature sensitivity is considered below) so that equation (3) reduces to

$$\mathrm{EU}(m) \propto n m^{3/4}. \tag{5}$$

We use this equation to derive relative EU estimates for all trilobite and brachiopod species in each sample. As with biomass, EU estimates are summed to produce an estimate of the total EU of each group in each collection. Although we assume ¾ scaling of individual metabolic rate with body size, assuming the alternative hypothesis of ⅔ scaling (Dodds et al. 2001) does not change the observed patterns significantly.

Predicted Abundance.—The positive scaling of individual EU with body size imposes a fundamental constraint on population density: if total energy availability is constant across all body size classes, then population density is expected to scale approximately as the inverse of body size (Damuth 1981, 1987b; Brown 1995; Kerr and Dickie 2001; Cohen 2003). Although the noise in this relationship is very high, it provides a first-order prediction of the expected population density (N) of a taxon:

$$N(T) = B_0 e^{-1/kT} m^{-3/4}, \tag{6}$$

which reduces to

$$N \propto B_0 m^{-3/4} \tag{7}$$

within a given environment with constant temperature, and

$$N \propto m^{-3/4} \tag{8}$$

for taxa belonging to the same clade and inhabiting the same environment. It is not possible to estimate relative abundances without size data for all taxa in each collection (which we do not have), because the *relative* abundance of any taxon is influenced by the abundance of all other taxa in the collection. However, the expected *ratio* of trilobite individuals to brachiopod individuals is dimensionless and unaffected by the abundances of other taxa. We therefore used equation (7) to predict the trilobite:brachiopod ratio for each collection only on the basis of the sizes of constituent taxa. Having no basis for estimating the normalization constant (B_0) for trilobites or brachiopods, we make the simplifying assumption that it is the same for both of these groups. Difference in B_0 would skew the ratio one way or another, but because all collections would be equally affected, this cannot distort predicted *trends* in the ratio, which are our primary concern.

Treatment of Missing Values.—All of the stratigraphic units included in our analysis are known to contain both trilobites and brachiopods, but trilobites occur in only 63% of Late Ordovician collections (versus 100% in the Early Ordovician), and brachiopods occur in only 74% of Early Ordovician collections (versus >99% in the Late Ordovician). This is not surprising: given the small size of many collections, rare taxa are likely to go unsampled. To avoid the problems associated with zeroes in the data set (dividing by zero, or plotting zeroes on a logarithmic scale), zeroes were assigned arbitrary values approximately one order of magnitude lower than the lowest actual value in the data set. Thus, if no brachiopods occurred in a collection it was assigned a brachiopod relative richness of 0.01, a relative abundance of 0.001, a biomass of 0.01, an EU of 0.01, and a predicted population density of 0.0001. An alternative approach is to combine collections by formation and calculate relative abundance, biomass, and EU from these pooled collections. This substantially reduces the number of data points but eliminates the need to account for missing values. Trends observed in pooled collections are very similar to those observed when all collections are treated independently.

Results

Consistent with previous studies, the average relative abundance of trilobites decreases by an order of magnitude between the Early Ordovician (I1–I2) and the Late Ordovician (M1–C2), whereas that of brachiopods increases (Fig. 2A,B). Trilobites constitute an average 58% of individuals in Early Ordovician collections, but only 4% of individuals in the Late Ordovician, whereas brachiopods go from an average of 19% in the Early Ordovician to 77% in the Late Ordovician. Relative genus richness trends are similar (Fig. 3A,B), though because of the low richness of all taxa in most samples (median genus richness = 6), they vary over a comparatively limited range.

The average body sizes of both trilobites and brachiopods increase substantially through the Ordovician (Churchill-Dickson 2001; Stempien et al. 2005; Novack-Gottshall 2008a) and this is expressed in our data set (Fig. 4A,B). Consequently, trends in biomass depart quite strikingly from relative richness and abundance trends (Fig. 5A,B). Most notably, the sharp decline in relative abundance of trilobites is not mirrored by biomass estimates: though total within-sample trilobite biomass varies over five orders of magnitude in the sample set as a whole, the average biomass of trilobites in Late Ordovician collections is within an order of magnitude of the Early Ordovician average.

The sharp increase in average trilobite body size in the upper Middle and Late Ordovician is largely attributable to the widespread occurrence of the exceptionally large asaphid genus *Isotelus*. This exclusively Laurentian genus includes the largest known trilobite species (*I. rex*), which attained lengths of up to 72 cm (Rudkin et al. 2003). Though this species does not appear in our data set, the four spe-

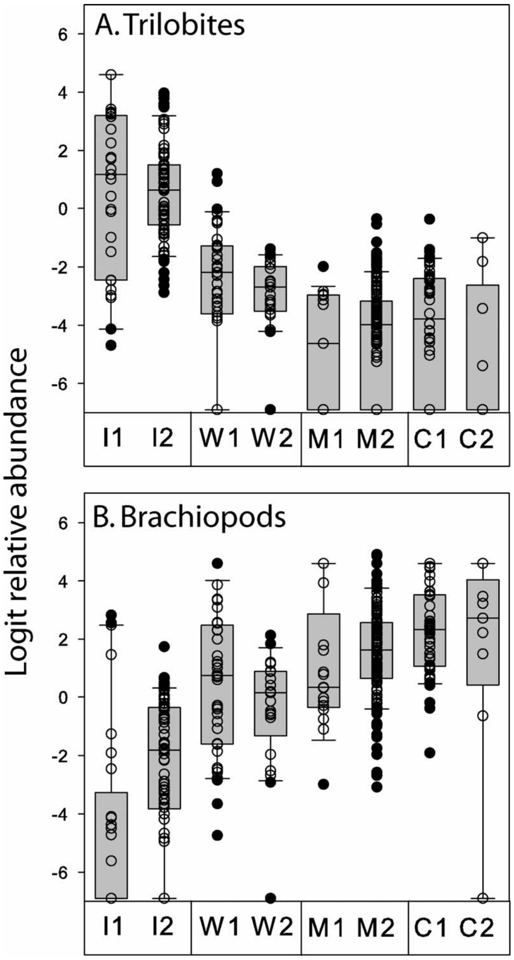

FIGURE 2. Temporal trends in the relative abundance of trilobites (A) and brachiopods (B) in shallow to deep subtidal mixed carbonate-clastic settings. The relative abundance of each group is calculated as a proportion of all individuals in the collection (including trilobites, brachiopods, and other taxa). When either group was entirely missing from a collection, it was arbitrarily assigned a relative abundance of 0.001. Relative abundances for each group are logit-transformed. The ends of the boxes mark the positions of the first and third quartiles, horizontal lines mark the median, whiskers extend 1.5 times the interquartile range (IQR) below the first and above the third quartile. Open circles are collections that fall less than 1.5 · IQR above or below the median; filled circles are outliers. Time bins are as follows: Ibexian 1 = 489.0–476.5 Ma, Ibexian 2 = 476.5–472 Ma, Whiterockian 1 = 472–470 Ma, Whiterockian 2 = 470–460.5 Ma, Mohawkian 1 = 460.5–454.5 Ma, Mohawkian 2 = 454.5–451 Ma, Cincinnatian 1 = 451–448.5 Ma, Cincinnatian 2 = 448.5–444 Ma.

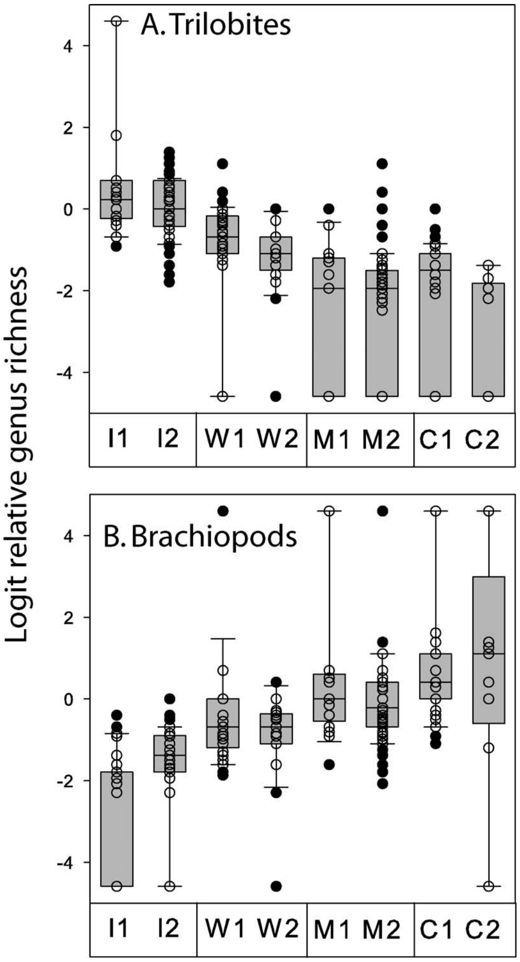

FIGURE 3. Temporal trends in the relative genus richness of trilobites (A) and brachiopods (B) in shallow to deep subtidal mixed carbonate-clastic settings. The relative richness of each group is calculated as a proportion of all genera in the collection (including trilobites, brachiopods, and other taxa). When either group was entirely missing from a collection, it was arbitrarily assigned a relative richness of 0.01. Relative richnesses for each group are logit-transformed Boxes, whiskers, circles, and time bins as in Figure 2.

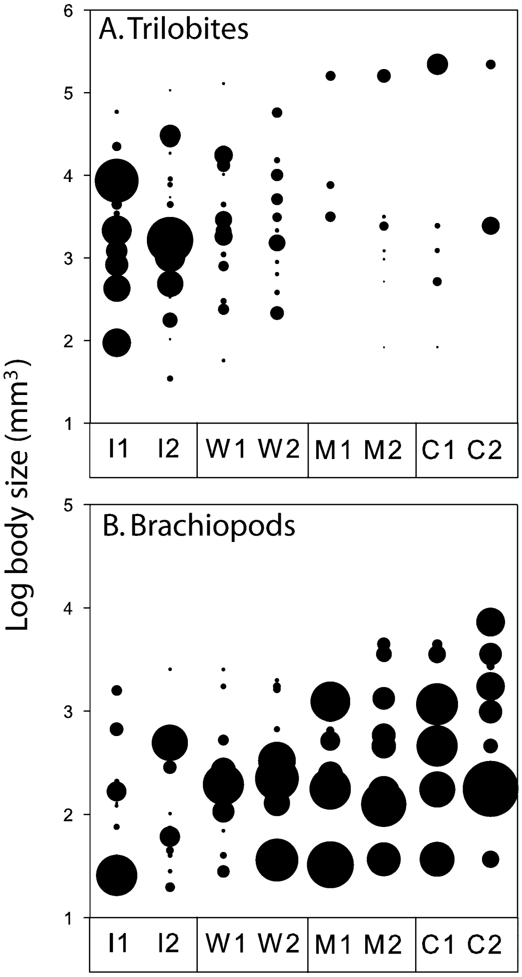

FIGURE 4. Temporal trends in the body size distributions and relative abundances of trilobites (A) and brachiopods (B) in shallow to deep subtidal mixed carbonate-clastic settings. The vertical axis is $\log_{10}$ estimated biovolume, and the bubble marking the position of each species is scaled to its average relative abundance in collections. The prominent gap in trilobite body size distribution during the Late Ordovician occurs between very large *Isotelus* species and moderate-sized ceraurid, calymenid, and proetid species. Time bins as in Figure 2.

cies that do, *I. gigas*, *I. copenhagenensis*, *I. brachycephalus*, and *I. maximus*—though *I. brachycephalus* and *I. maximus* are rarely differentiated in published data sets and may not in fact be discrete species (Rudkin et al. 2003)—all attain average body sizes nearly two orders of magnitude above the median trilobite body size. Unsurprisingly given the expected inverse relationship between body mass and population density, these trilobites are comparatively uncommon (Fig. 4A) and are absent in many samples from stratigraphic units in which they are known to occur. Nevertheless, they constitute a large proportion of all trilobite individuals in late Middle and Late Ordovician samples and their average size is such that the *average* biomass of Late Ordovician samples is comparable to that of Early Ordovician samples even when these absences are included.

The average estimated EU of trilobites also shows no secular trend (Fig. 6A), whereas that

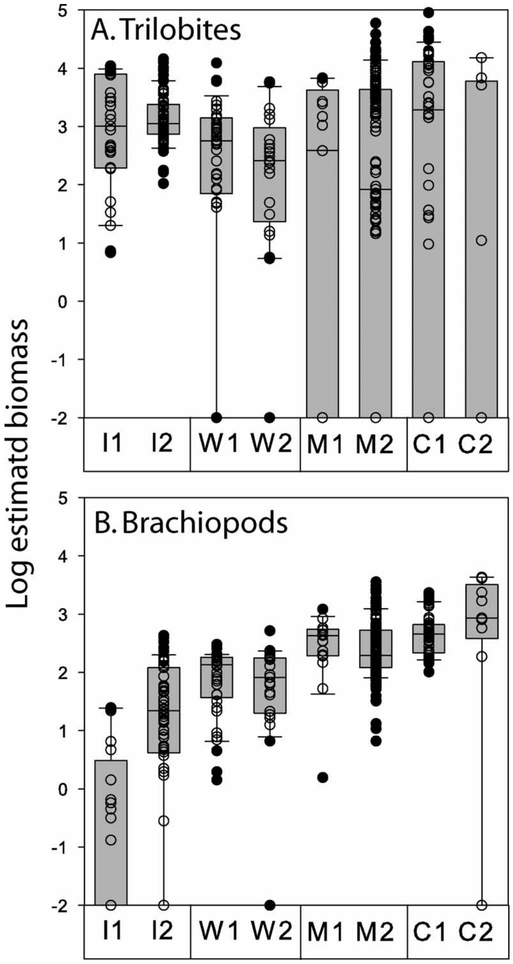

FIGURE 5. Temporal trends in the estimated standing biomass of trilobites (A) and brachiopods (B) in shallow to deep subtidal mixed carbonate-clastic settings. Biomass is calculated as mean body size multiplied by relative abundance, and the resulting biomass estimates are summed for all taxa in each group. If a group was entirely missing from a collection, it was arbitrarily assigned a biomass of 0.01. Boxes, whiskers, circles, and time bins as in Figure 2.

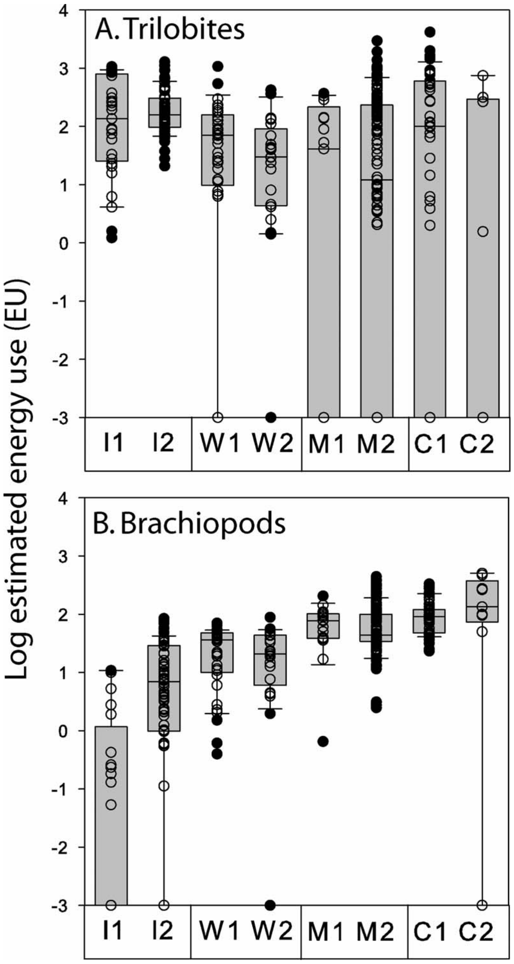

FIGURE 6. Temporal trends in the estimated energy use (EU) of trilobites (A) and brachiopods (B) in shallow to deep subtidal mixed carbonate-clastic settings. EU is calculated as mean body size to the ¾ power multiplied by relative abundance, and the resulting EU estimates are summed for all taxa in each group. If a group was entirely missing from a collection, it was arbitrarily assigned an EU of 0.01. Boxes, whiskers, circles, and time bins as in Figure 2.

of brachiopods increases substantially (Fig. 6B). In estimating EU, however, the temperature-sensitivity of metabolic efficiency (eq. 3) introduces a complicating factor. We have minimized the effects of *latitudinal* variation in our data set by including only collections from temperature-sensitive, carbonate-dominated depositional settings within tropical to subtropical latitudes, but there is considerable evidence of a long-term cooling trend throughout much of the Late Ordovician of Laurentia (Patzkowsky et al. 1997; Pope and Steffen 2003; Herrmann et al. 2004; Saltzman and Young 2005), and several of the Late Ordovician units sampled in our database have been interpreted as cool-water carbonates (Pope and Read 1995; Holland and Patzkowsky 1996). The earliest evidence of significant cooling in Laurentia occurs in the late Mohawkian (Pope and Steffen 2003; Saltzman and Young 2005) and includes a shift to more positive $\delta^{18}O$ and $\delta^{13}C$ values (Shields et al. 2003), expansion of cherts and other upwelling-associated lithologies along the southern margin, and a shift from tropical to temperate-type carbonate sedimentation in the Taconic foreland and adjacent cratonic seaway. Ocean circulation models suggest that average sea-surface temperatures along the southern margin of Laurentia and in the interior seaway may have been as low as 18–20°C (Herrmann et al. 2004), despite its tropical-to-subtropical position. Assuming, by comparison with modern tropical seas, an average sea-surface temperature of 27°C during deposition of Ibexian-Whiterockian and lower Mohawkian tropical carbonates, this suggests a 7–9°C cooling in the Late Mohawkian. We use equation (4) to evaluate the effect of a 10°C cooling on series-level trends in trilobite EU (Fig. 7).

This has some effect on estimated EU trends for both trilobites and brachiopods. Under this model, trilobites show a slight decline in estimated EU (Fig. 7A), though the decline is neither as coherent nor as large in magnitude as the decline in relative abundance (Fig. 2A). The estimated EU of brachiopods remains fairly constant from the Whiterockian on under this model (Fig. 7B), whereas under the constant temperature model there is a distinct, sustained increase from the Middle (W1–W2) to the Late (M1–C2) Ordovician. These results are suggestive, but we emphasize that this model builds in multiple assumptions and simplifications regarding quite poorly controlled variables, and hence should be viewed with a good deal of skepticism. We also point out that trilobite biomass estimates remain roughly constant, and brachiopod biomass estimates increase significantly, from the late Middle Ordovician (W2) to the early Late Ordovician (M1). Coming as this does *before* the onset of mid-Mohawkian cooling, it suggests that cooling by itself does not provide an adequate explanation for the observed trends.

The increasing average body size of trilobite individuals raises the possibility that the declining relative abundance of trilobites in this data set is, in part, a consequence of the inverse association between abundance and body size. This can be evaluated by comparing the observed trend in the ratio of trilobite to brachiopod individuals to the trend predicted by body size (eq. 7). As a comparison, we also calculated the ratio of trilobite to brachiopod genera in each collection; this gives the expected ratio of trilobite to brachiopod individuals if all taxa are represented by equal numbers of individuals (i.e., evenness = 1), with no association between size and abundance.

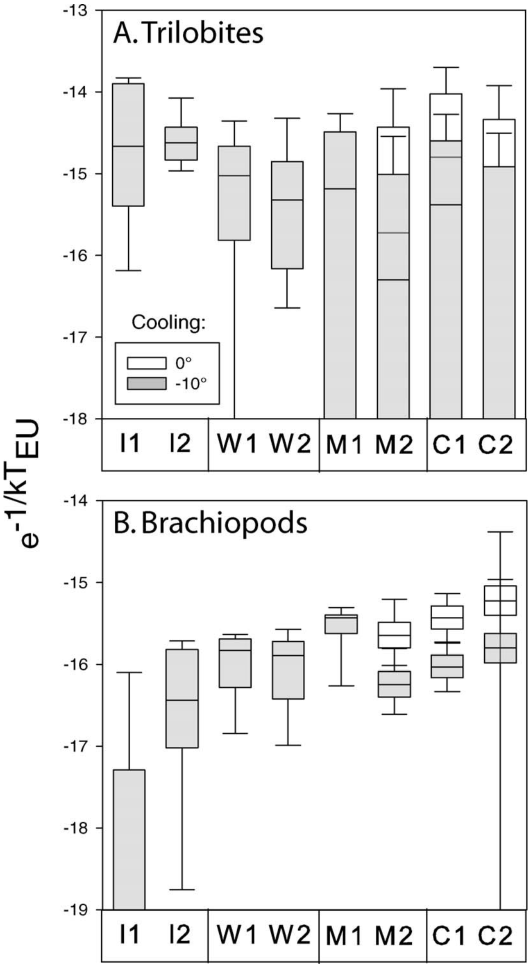

FIGURE 7. Impact of a hypothetical 10°C cooling in the mid-Mohawkian on estimated energy use of trilobites (A) and brachiopods (B). Open boxes represent the observed trend if a uniform average temperature of 27°C is assumed; filled boxes represent the trend if an average temperature of 17°C is assumed from the mid-Mohawkian on. The vertical axis is scaled by multiplying EU by $e^{-1/kT}$, and hence the units are arbitrary. Boxes, whiskers, and time bins as in Figure 2.

The trends in average trilobite:brachiopod ratio predicted by the size-dependent and size-independent approaches are both closely correlated with the observed trend (Fig. 8); however, the slope is much closer to one when the average trilobite:brachiopod ratio is regressed on the average ratio predicted by the

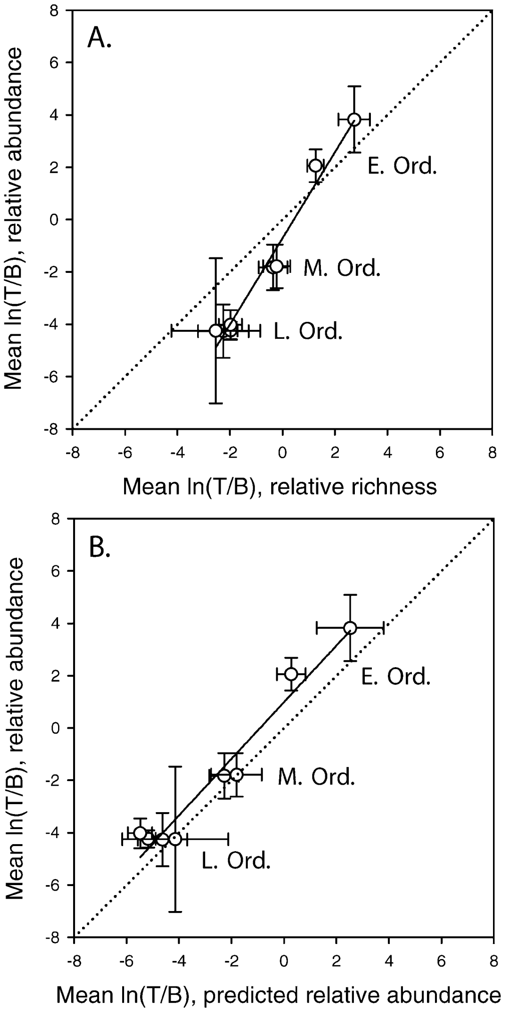

FIGURE 8. The average ratio of trilobite individuals to brachiopod individuals for each time bin plotted against the average ratio of trilobite genera to brachiopod genera (A) and against the average ratio of trilobite individuals to brachiopod individuals predicted by body size distributions (B). Bars represent 95% confidence intervals for the mean. Body size and richness provide a better prediction of abundance trends than does richness alone.

size-dependent model than it is when the average trilobite:brachiopod ratio is regressed on the average ratio predicted by the size-independent model. The size-independent model significantly underestimates the magnitude of the decrease in the trilobite:brachiopod ratio between the Early and Late Ordovician, whereas the size-dependent model predicts it accurately. The size-dependent model does have an intercept significantly greater than zero, indicating that it consistently overestimates the trilobite:brachiopod ratio, especially in the Early Ordovician. This suggests that the normalization factor associated with size-abundance scaling may be higher for brachiopods than for trilobites.

Discussion

Preservation of Abundance–Body Size Relationships.—Abundance and body size patterns in modern clades and ecosystems are a contentious subject in part because accurate measurement is difficult (Blackburn and Gaston 1997), and such problems are obviously compounded in the fossil record. Time-averaging, transport, and differential preservation potential, life span, and mode and rate of shell production all have potentially severe effects on the ecological fidelity of abundance and body size data in fossil assemblages. Nonetheless, live-dead comparisons of mollusk communities have shown surprisingly strong agreement in rank-order abundance between skeletal assemblages and the communities from which they derive (Kidwell 2001, 2002), suggesting that at least within single clades it may be possible to track abundance trends in the fossil record. Brachiopods are good candidates for such study because of their relatively durable low-organic calcite shells. Trilobites are also readily preservable, but interpretation of trilobite abundance trends is complicated by the fact that they regularly molted as they grew. It is unclear how this should affect size-abundance relationships—on one hand, smaller species are likely to have had shorter generation times and thus to have contributed disproportionately to time-averaged shell accumulations; on the other hand, larger species were likely longer-lived and thus presumably produced more molts per individual over their lifetime. This issue may ultimately be addressed by comparing abundance to estimated growth rate in species for which both types of data are available, but in the absence of such data we assume that total molt contribution is invariant with respect to body size.

One of the most fundamental aspects of ecosystem structure is that maximum population density decreases as a function of body size—on average, small organisms are more numerous than large ones. This relationship, appar-

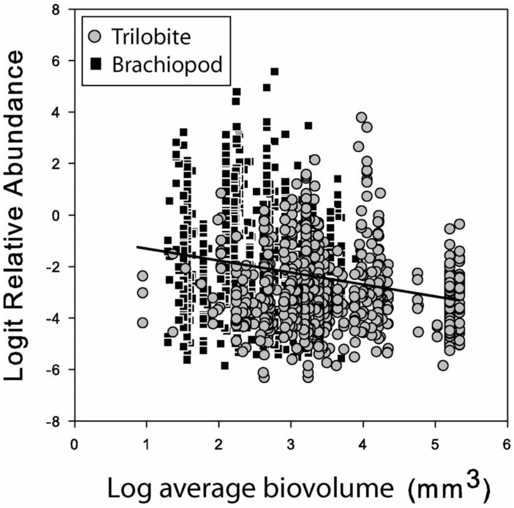

FIGURE 9. Logit-transformed relative abundance versus log-transformed average body size for all trilobite and brachiopod occurrences in the data set. There is a weak but significant negative association between body size and relative abundance (slope $= -0.46$, $p = 0.009$).

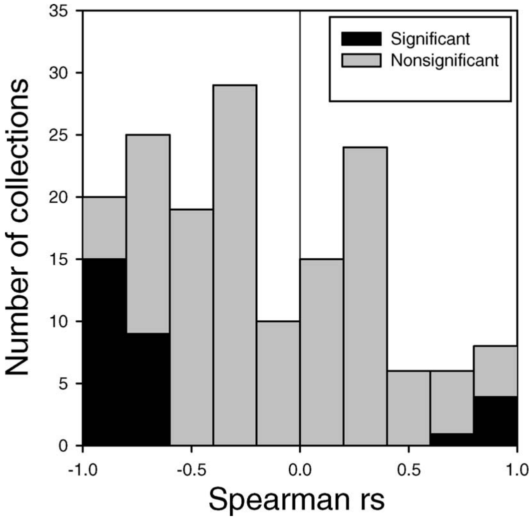

FIGURE 10. Histogram of Spearman *rs* values for the correlation between body size and rank abundance for all collections containing at least four trilobite and/or brachiopod genera. Negative *rs* scores are significantly more common than positive scores, indicating that the expected scaling of abundance with body size is preserved in the majority of collections. Black bars represent *rs* score that are significant at the 95% confidence level, and gray bars represent insignificant scores. The low proportion of significant scores is expected given the small numbers of taxa in most collections.

ent in a wide array of marine and terrestrial ecosystems, reflects fundamental energetic constraints imposed by the positive scaling of individual EU with body size (Damuth 1981, 1987b; Brown 1995; Kerr and Dickie 2001; Cohen 2003). Thus, examining the relationship between body size and relative abundance in our data set constitutes a simple test of its first-order ecological fidelity. Plotting the logit of relative abundance against the log of mean body size for all occurrences in the data set (Fig. 9) suggests that there is a signal, however degraded, of original abundance structure. Although variance is very high and most taxa tend to be rare in all size classes, both maximum and average relative abundance decrease with increasing body size. A permutation test on the slope of this relationship ($=-0.46$) shows that it is significantly nonrandom ($p = 0.009$), although the difference in units (logit abundance versus log biovolume) makes it difficult to directly compare this slope to the −¾ log-log slope predicted by the energetic equivalence rule.

The small size of most collections in our database (median number of individuals = 61) constrains relative abundance to vary only over two orders of magnitude whereas body sizes span six orders of magnitude, making it difficult to test for specific scaling relationships. Variation in sample size also introduces significant noise into relative abundance patterns: the relative abundance of the rarest taxon in a collection of 50 individuals may be an order of magnitude higher than the relative abundance of the rarest taxon in a collection of 500 individuals. An alternative approach that eliminates this problem is to test for size-structuring within each collection, rather than among all taxon occurrences collectively. We therefore calculated Spearman rank-order correlation coefficients (*rs*) for the association between relative abundance and mean body size for each collection that included at least four brachiopod and/or trilobite taxa. If there is no inverse association between abundance and size, *rs* values should show a mode centered on zero. There is, however, a clear tendency toward negative *rs* scores: 64% of all collections have negative *rs* scores, and this figure rises to 83% if only statistically significant *rs* scores are considered (Fig. 10). The potential for size-related biasing of relative abundance patterns in the fossil record is an

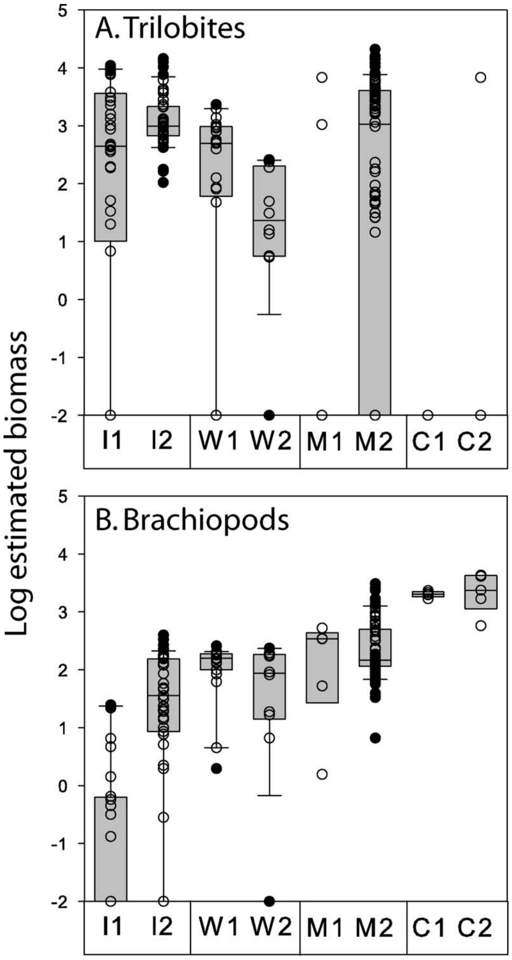

FIGURE 11. Temporal trends in the estimated standing biomass of trilobites (A) and brachiopods (B) in shallow subtidal collections only. Biomass calculated as in Figure 4; boxes, whiskers, circles, and time bins as in Figure 2.

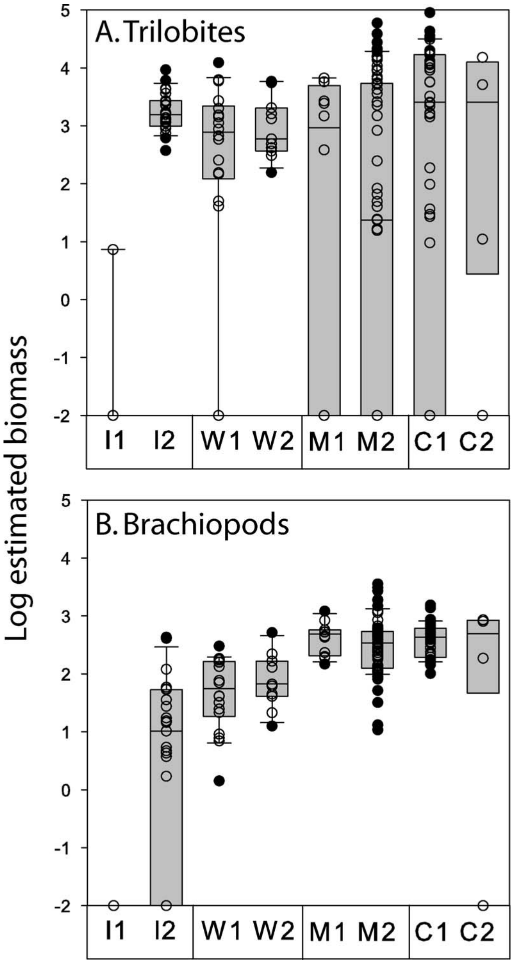

FIGURE 12. Temporal trends in the estimated standing biomass of trilobites (A) and brachiopods (B) in deep subtidal collections only. Biomass calculated as in Figure 4; boxes, whiskers, circles, and time bins as in Figure 2.

important subject for more detailed investigation with larger collections, but at present we see little evidence that abundance trends in this data set are significantly size-biased.

Environmental Coverage.—Our data set is intentionally limited to mixed carbonate-clastic units above maximum storm wave base, and it excludes the deep slope and basinal environments in which trilobites may have remained dominant elements of the fauna into the Late Ordovician (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985). Within this relatively narrow range bathymetric coverage is uneven—most Early Ordovician collections represent shallow subtidal environments (above normal wave base), whereas most Late Ordovician collections are from deep subtidal collections (between normal wave base and maximum storm wave base). Both shallow and deep subtidal collections show similar trends in estimated biomass, however (Figs. 11, 12), and hence it is unlikely that the composite trend is strongly influenced by environmental heterogeneity.

Geographic Coverage and Generality of Results.—Many of the units that have figured in previous studies of Ordovician paleoecological trends and evolutionary faunas are included in our database. Coverage of the Upper Ordovician strata of the Appalachian foreland and adjacent cratonic sea is particularly heavy. The richly fossiliferous rocks of this region contain a quite low-diversity and low-abundance trilobite fauna (only nine genera occur in our Mohawkian data set, and seven in the Cincinnatian), and this paucity has been the basis for previous suggestions that the ecological significance of trilobites decreased through the Ordovician (Miller et al. 1998). Thus, although it is geographically limited to two broad regions, the data set is appropriate for testing this hypothesis. Suitable whole-fauna abundance and body size data are not available from other well-studied Upper Ordovician strata in Canada and the Midwestern United States (Westrop and Adrain 1998a; Adrain et al. 2000; Hunda et al. 2003; Amati 2004), but given the comparatively high species richness of trilobites in these units it is unlikely that the relative abundance of trilobites is lower than it is in the eastern United States.

It is also noteworthy that moderately to extremely large species of *Isotelus* occur in many of these units, including the largest trilobite ever described, *I. rex*, in the Cincinnatian of Manitoba (Rudkin et al. 2003). The temporal and geographic distribution of large Isotelus species in eastern North America has been recently reviewed (Rudkin et al. 2003); in the Cordilleran belt, several Middle and Late Ordovician *Isotelus* species are known from silicified material (Chatterton and Ludvigsen 1976; Ross et al. 1980; Hunda et al. 2003) that often consists primarily of small early ontogenetic stages, so that the average adult size of these species cannot be reliably estimated from published plates. Exceptionally large species are present in at least some Cordilleran units—for instance the Whiterockian to early Mohawkian species *I. copenhagenensis*, which occurs in our collections from Nevada, attained a maximum length of at least ~20 cm, according to extrapolation from a figured pygidium (Ross and Shaw 1972).

Implications for Ordovician Trends in Animal Biomass.—Bambach (1993) argued that the aggregate standing biomass of marine invertebrates has increased through the Phanerozoic. Although he did not specifically discuss biomass increase in the Ordovician, our results, along with other recent work (Novack-Gottshall 2008a) suggest that the dramatic increase in the diversity of skeletonized marine invertebrates during the Ordovician was accompanied by a substantial increase in their standing biomass. Our data are obviously limited to two well-skeletonized groups, but the Ordovician increase in the depth and intensity of bioturbation (Droser and Bottjer 1989) is evidence that the biomass of soft-bodied infaunal burrowers also increased. Whether this trend reflects an increase in overall primary productivity, in the nature of primary producers, or in the metabolic efficiency of consumers (Payne and Finnegan 2006) remains an open question.

Implications for the Nature of Ordovician Ecological Restructuring.—Our results provide little support for the hypothesis that trilobites were in any way actively displaced from benthic habitats by the expansion of the Paleozoic Fauna. Because of an increase in the average body mass of sampled individuals, estimates of the most fundamental metrics of ecological significance—biomass and energy use—are fairly constant for trilobites despite an order-of magnitude decline in the relative abundance of this group. This does not necessarily imply that there were no significant ecological interactions between trilobites and members of the Paleozoic EF (or for that matter, the Modern EF). Any such interactions would almost necessarily have been rather diffuse, however—there is little evidence of predator-prey interactions, and trilobites occupied a quite different region of ecospace than the members of the Paleozoic EF, most of which were sessile suspension feeders (Bush et al. 2007; Novack-Gottshall 2007). Given this, we favor the interpretation that the Paleozoic EF diversified not by outcompeting the Cambrian EF but by evolving to take advantage of resources (particulate organic matter in the water column, in particular) that were underutilized by the members of the Cambrian EF.

The trend in body size distribution of trilobites in our data set does suggest the possibility that the ecological roles of trilobites may have changed quite significantly during the Ordovician, a notion that is also supported by other lines of evidence. Foote (Foote 1991; Miller and Foote 1996) found that the morphological diversity of trilobites increased significantly between the Early and Late Ordovician, suggesting a comparable increase in ecological diversity. Fortey and Owens (1999) have made the functional morphological argument that trilobites with hypostomes lacking a skeletal attachment to the cranidium were likely detritivores, whereas those with hypostomes firmly braced against the cranidium were probably predators and scavengers. The former group taxonomically and numerically dominates many trilobite communities in the Middle–Late Cambrian and Early Ordovician, but trilobites with attached hypostomes (of which *Isotelus* is a particularly well-known example) are taxonomically dominant by the Late Ordovician. If Fortey and Owens' model is correct, this trend implies an increase in mean trophic level for the clade as a whole during the Ordovician. Because less energy is available at higher trophic levels this would, all else being equal, force a decline in abundance even in the absence of a trend toward larger body sizes. However, absent better information about both trilobite feeding habits and Ordovician productivity trends, this line of argument remains speculative.

Our data set is restricted to two broad geographic regions and a narrow range of environments, and hence it is not sufficient to generalize about clade-level body size trends. But recent studies of continental and global-scale body size distributions have found significant increases in the average body size of trilobites (Churchill-Dickson 2001, personal communication 2005; Novack-Gottshall 2008a), brachiopods (Harper et al. 2004a; Stempien et al. 2005), and bivalves (Stempien et al. 2005) through the Ordovician. Brachiopods also diversify explosively (Harper et al. 2004a) and bivalves diversity steadily (Miller and Sepkoski 1988) through this interval, but both the alpha (within-habitat) and global genus diversity of trilobites remains roughly invariant (Westrop and Adrain 1998a; Adrain et al. 2000; Sepkoski 2002). Despite two major family-level turnover pulses within the Ordovician (Adrain et al. 2004), trilobite communities appear to have been ''species-saturated''—at or near carrying capacity—from the Middle Cambrian through the mid-Silurian, excepting depauperate post-extinction communities (Adrain et al. 2000).

Together with the increase in average body size, this saturation suggests a novel explanation for the apparent decline in trilobite abundance. An increase in average cranidium length from ~6.5 mm to ~9.5 mm, observed in multiple Laurentian families (L. Churchill-Dickson personal communication 2005) can be extrapolated with the geometrical approximations discussed above to a roughly threefold increase in average body mass. Assuming ¾ power scaling of individual metabolic rate with body size and constant food availability, a threefold increase in body mass would necessarily be accompanied by a ~57% decrease in population density ($[1/3]^{3/4} = .43$). Thus, it may be that the declining abundance of trilobites in the Ordovician is at least in part a simple consequence of Cope's Rule—the frequently observed tendency of lineages to increase in size through time (Stanley 1973; Jablonski 1996). This suggestion is quite speculative, but the general relationships among body size, diversity, and abundance trends over macroevolutionary time scales are intriguing areas for further research.

Summary

The well-documented Ordovician decline in the relative abundance of trilobites in shallow to deep subtidal level-bottom assemblages (Fig. 2) is not paralleled by estimates of trilobite biomass or energy use (Figs. 5, 6), which instead show relative stability throughout the Ordovician. This stability is attributable to the increasing average body size of trilobites (Fig. 4), and in particular the widespread occurrence of species of the genus *Isotelus* in Middle and Late Ordovician collections. Brachiopods show increases in relative abundance, richness, mean body size, and estimated biomass and energy use throughout the Ordovician. There is thus little evidence that, at the local level, the expansion of the brachiopods and other members of the Paleozoic Evolutionary Fauna came at the expense of trilobites in Laurentia. Rather, the aggregate standing biomass of benthic communities increased as the biomass (and by inference the energy use) of trilobites remained approximately constant and that of Paleozoic EF members rose substantially. Although they show no strong trend in standing biomass or inferred energy use, other lines of evidence do suggest that trilobites were active participants in Ordovician biodiversification, evolving new morphologies and new ecological strategies over the course of the interval. These data demonstrate that temporal trends in biomass may be substantially decoupled from trends in relative abundance, and hence caution should be used in drawing explicit or implicit energetic inferences from abundance data alone.

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