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Metabolic dominance of bivalves predates brachiopod diversity decline by more than 150 million years

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Brachiopods and bivalves feed in similar ways and have occupied the same environments through geological time, but brachiopods were far more diverse and abundant in the Palaeozoic whereas bivalves dominate the post-Palaeozoic, suggesting a transition in ecological dominance 250 Ma. However, diversity and abundance data alone may not adequately describe key changes in ecosystem function, such as metabolic activity. Here, we use newly compiled body size data for 6066 genera of bivalves and brachiopods to calculate metabolic rates and revisit this question from the perspective of energy use, finding that bivalves already accounted for a larger share of metabolic activity in Palaeozoic oceans. We also find that the metabolic activity of bivalves has increased by more than two orders of magnitude over this interval, whereas brachiopod metabolic activity has declined by more than 50%. Consequently, the increase in bivalve energy metabolism must have occurred via the acquisition of new food resources rather than through the displacement of brachiopods. The canonical view of a mid-Phanerozoic transition from brachiopod to bivalve dominance results from a focus on taxonomic diversity and numerical abundance as measures of ecological importance. From a metabolic perspective, the oceans have always belonged to the clams.

1. Introduction

Brachiopods and bivalves feed in similar ways and have occupied the same environments through geological time, but their evolutionary trajectories contrast sharply. Brachiopods are far more diverse and abundant in Palaeozoic rocks, whereas bivalves are predominant in post-Palaeozoic strata [1,2]. This reversal in relative taxonomic diversity and numerical abundance has long been equated with a transition in ecological dominance [1–7]. Abundance and diversity are the most accessible and widely used metrics of ecological dominance in the fossil record [1], but they are incomplete proxies. Ecosystems function through the transfer of mass and energy rather than via the simple accumulation of organisms [8]. Substantial differences in both shell size to soft tissue mass ratios and mass- and temperature-normalized metabolic rate between living species of bivalves and brachiopods [9,10] suggest that taxonomic diversity and numerical abundance alone may not adequately capture relative ecological importance for bivalves and brachiopods. Quantification of metabolic activity by bivalves and brachiopods can provide a complementary, and potentially more relevant, perspective on the relative ecological importance of brachiopods and bivalves in benthic marine ecosystems over geological time.

To a first order, metabolic rates in animals are related to body size (soft tissue mass), temperature and clade affinity and can thus be constrained even for fossil organisms [11,12]. Here, we reexamine the evolutionary histories of bivalves and brachiopods through the lens of energy metabolism using newly compiled body size data for 6066 genera of bivalves and brachiopods coupled to occurrence and abundance data from the Paleobiology Database (PaleoDB).

2. Data and methods

(a) Body size data

For each taxon, we measured each of the three major shell axes using the specimens illustrated in the *Treatise on Invertebrate Paleontology*. For brachiopods, all measurements were obtained from the revised edition of the *Treatise* [13]. The brachiopod volumes of the *Treatise* illustrate 4802 species from 4358 genera and subgenera. The bivalve volumes of the *Treatise* [14] illustrate 3329 distinct species, each representing a distinct genus or subgenus. Additional bivalve size data were obtained from Huber's [15] compendium of living bivalve species. To improve both taxonomic and temporal resolution, subgenera were elevated to genus status for all calculations.

For maximum completeness, we used the longest linear dimension of the largest specimen for each genus in all calculations. In our data, the longest axis of any given shell is highly correlated with its volume (bivalves: $R^2 = 0.93$; brachiopods: $R^2 = 0.97$; electronic supplementary material, table S1), demonstrating that length is a reliable proxy for overall shell size. Previous studies have also shown that maximum linear dimension is highly correlated with shell volume [16] and soft tissue mass [11,17]. Because most variation in body size is among species and genera rather than within them [18,19] and because the sizes of illustrated specimens typically correlate with the mean and maximum of populations from bulk samples [20,21], the sizes of specimens illustrated in the *Treatise* and other compendia can be informative of long-term evolutionary trends even if they are insufficient to resolve short-term variations.

(b) Stratigraphic range data

In our primary data treatment, we defined stratigraphic ranges based on the first and last reported stage-resolved occurrences of each genus in the PaleoDB (<http://www.paleodb.org>; downloaded on 10 May 2013). Using this approach, we were able to match body size data to stage-resolved fossil occurrence information for 2563 genera of brachiopods and 1418 genera of bivalves, representing 73% and 47% of PaleoDB brachiopod and bivalve genera, respectively.

In a supplementary data treatment, we defined stratigraphic ranges based not only on the PaleoDB but also on reports from the *Treatise* and Sepkoski's [22] compendium of genus stratigraphic ranges. In this treatment, we took the earliest first occurrence and the latest last occurrence across the sources as the complete stratigraphic range of the genus. Using this approach, we were able to match body size data to stage-resolved stratigraphic range information for 3944 genera of brachiopods and 2122 genera of bivalves, representing 89% of brachiopod genera and 64% of bivalve genera reported in the *Treatise*.

(c) Fossil occurrence data

We downloaded fossil occurrence data for bivalves and brachiopods from the PaleoDB. We were able to match our size data to 164 402 stage-resolved occurrences (81 300 brachiopod occurrences and 83 102 bivalve occurrences), where an occurrence is defined as a unique genus–locality–stage combination. In total, we were able to match size data to 91.84% of all brachiopod occurrences and 85.38% of all bivalve occurrences in the PaleoDB. We were further able to match our size data to 140 288 specimens from 925 collections in the PaleoDB that contain

abundance data for both bivalves and brachiopods. We excluded the Cambrian Period, the oldest period of the Phanerozoic, from our primary data treatment because bivalves and the typical 'articulate' brachiopods were rare and taxonomically depauperate during the earliest Phanerozoic, but including the Cambrian does not affect our general findings (electronic supplementary material, figure S2). Raw data files used for all analyses are permanently archived in the Stanford Digital Repository (<http://purl.stanford.edu/hs422jm3330>).

(d) Assignment of feeding mode

To compare metabolic rates only within shared feeding modes, we coded each genus with respect to its primary feeding mode following the scheme of Bush *et al.* [23]. Each taxon was assigned to its primary feeding mode as one of six possible feeding categories (suspension, surface deposit, mining, grazing, predatory or other) based on previously published studies [15,24,25] (http://eusmilia.geology.uiowa.edu/database/bivalves/Bivalve_eco.html).

(e) Calculation of metabolic rates

We used stratigraphic range, fossil occurrence and specimen count data from individual fossil collections to calculate mean metabolic rate per genus, per occurrence and *per capita* for each geological stage. In the case of *per capita* measures, we calculated a mean *per capita* metabolic rate for each collection, and then a mean metabolic rate for the stage as the arithmetic mean of all collection-level arithmetic means. We calculated the mean per genus metabolic rate in three ways: (i) using only stratigraphic range information from the PaleoDB; (ii) using the PaleoDB but only including the genus for stages in which it had a known fossil occurrence as opposed to all stages between the oldest and the youngest occurrences and (iii) using all available stratigraphic range information (PaleoDB, *Treatise*, Sepkoski's compendium) and assuming each genus to be present during all stages between its first and last known occurrence.

We calculated metabolic rate for each genus, occurrence or specimen following the formulation of Gillooly *et al.* [26]:

$$B_{\text{ind}} = b_0 e^{-E/kT} M^{3/4}, \quad (2.1)$$

where B_{ind} is the metabolic rate of the individual (in Watts), E is the typical activation energy of rate-limiting metabolic reactions (approx. 0.65 eV), k is Boltzmann's constant, T is absolute temperature (K) at which metabolism occurs (i.e. ambient temperature for marine invertebrate animals) and b_0 is a scaling constant. Based upon Brey's [27] database of respiration rates in marine invertebrate animals (summarized by [28]), we take b_0 to be $6.5 \times 10^{10} \text{W kg}^{-3/4}$ for articulate (i.e. rhynchonelliform) brachiopods, $5.6 \times 10^{10} \text{W kg}^{-3/4}$ for all other brachiopods, $1.4 \times 10^{11} \text{W kg}^{-3/4}$ for heterodont bivalves and $1.3 \times 10^{11} \text{W kg}^{-3/4}$ for all other bivalves. Based upon a compilation of data from the published literature ([9,29–35]; electronic supplementary material, table S2), we assume that ash-free dry mass (AFDM; in grams) scales as $8.0 \times 10^{-7} \times L^{3.34}$ for brachiopods and as $1.0 \times 10^{-5} \times L^{2.95}$ for bivalves, where L is the maximum linear dimension of the shell. We calculated the scaling coefficients and exponents relating length to AFDM for brachiopods and bivalves from the published coefficients, exponents and size ranges for individual species. Rather than simply taking the mean of the within-species coefficients and exponents, we

conducted an ordinary least-squares regression after representing each species by two datapoints, one at its reported minimum size and another at its reported maximum size. This approach allows us to identify any difference between the typical within-species relationship versus the aggregate among-species relationship. It was also necessary because previous studies report coefficients and exponents for the length–AFDM relationship but do not present tables of measurements for individual specimens. Fortunately, simply taking the mean values of species-level slopes and intercepts within each clade yields comparable results and so our findings are not sensitive to any difference between the typical within-species length–AFDM relationship and the aggregate among-species relationship. We further find that simply assuming a length–AFDM scaling exponent of 3.0 and only accounting for differences in the coefficient also yields comparable results.

(e) Sensitivity analysis

To address sensitivity of our results to the temperature dependence of metabolic rate, we analysed our data in three ways. First, we assumed that all taxa experienced the same temperature (15°C). Second, we assumed that global mean temperatures did not vary over geological time, but that a linear, 30°C temperature gradient has always existed from the equator to the poles. The strength of this meridional temperature gradient has varied over geological time, but we assumed a large and constant gradient for simplicity. Third, we assumed that both global mean temperature has varied following the palaeoclimate reconstruction of Royer *et al.* [36], and there has always existed a temperature gradient of 30°C from equator to pole. We used the last formulation as our primary data treatment.

To address sensitivity of our results to the scaling of shell length to soft tissue mass and clade-level differences in mass- and temperature-normalized metabolic rates, we analysed our data in three ways. First, we used published data (electronic supplementary material, table S2) to calculate scaling equations for AFDM to shell length in bivalves and brachiopods separately. Second, we analysed our data assuming that b_0 values did not differ between brachiopods and bivalves (using the bivalve value). Third, we analysed our data assuming that brachiopods have the same b_0 values and the same scaling of shell length to AFDM observed in bivalves. We used the first of these formulations as our primary data treatment. We view the last of these formulations as unrealistically conservative, given that we are aware of no evidence that brachiopod b_0 or length–AFDM scaling are as high as those in bivalves.

Finally, we investigated the sensitivity of our results to the presence or the absence of the largest and the smallest taxa in our dataset. The fossil record is commonly biased against the preservation and recovery of small species and specimens, particularly those less than 5–10 mm in maximum dimension [37–40]. We therefore reanalysed our data after excluding all taxa with a maximum linear dimension of less than 10 mm to determine the sensitivity of our result to the heterogeneous sampling of small species. In highly skewed datasets such as our length and metabolic rate data, arithmetic means can be highly sensitive to one or a few outliers. To determine the sensitivity of our results to the largest species, we reanalysed our data after excluding the largest 10% of occurrences from each stage.

3. Results

Although brachiopods were taxonomically and numerically dominant in Palaeozoic oceans, bivalves already used as much or more energy (figures 1 and 2). This finding holds even when restricting the comparison to bivalves that, like all brachiopods, are suspension feeders (electronic supplementary material, figure S1). When including genera with known stratigraphic ranges but lacking occurrences recorded in the PaleoDB, the transition to bivalve metabolic dominance occurs approximately 350 Ma (electronic supplementary material, figure S1). Since the beginning of the Triassic Period (*ca* 250 Ma), bivalves have been responsible for more than 95% of metabolic activity across the two clades by all measures (figures 1 and 2; electronic supplementary material, figure S1). Per genus, per occurrence and *per capita* measures all indicate that the mean metabolic rate increased by more than two orders of magnitude from the Ordovician (*ca* 465 Ma) to the present day (figure 3; electronic supplementary material, figure S2) and likely by another order of magnitude from the Cambrian to the Ordovician (electronic supplementary material, figure S2). Furthermore, the differences among metrics within a given time interval are far smaller than the increase over time (figure 3; electronic supplementary material, figure S2).

The close agreement between per genus, per occurrence and *per capita* measures of mean metabolic rate relative to temporal variation does not appear to result from taphonomic alteration of fossil assemblages. Using a published dataset of 519 species and 204 779 specimens of living marine bivalves collected from 211 sites in the Atlantic Ocean [41], we find that mean per genus, per occurrence and *per capita* metabolic rates differ only by a factor of two to five (electronic supplementary material, table S3), comparable to the spread among metrics in the fossil data (figure 3). By contrast, temporal variation in mean metabolic rate for our fossil data spans more than two orders of magnitude for all metrics. Further support for the reliability of rates calculated from fossil assemblages comes from living and fossil (Neogene) gastropod tropical shelf communities, which yield indistinguishable mean *per capita* metabolic rates [12]. Thus, not only does the long-term increase in metabolic rates in our dataset far exceed the variation among metrics, but fossil data do not appear to be strongly biased relative to rates calculated for living communities.

The magnitude and timing of the increase in mean metabolic rate are insensitive to uncertainties regarding ambient temperature, soft tissue mass of extinct organisms, per gram metabolic rates and the extremes of the size distribution. Accounting for the equator-to-pole temperature gradient and long-term variation in global average temperatures does not alter the first-order pattern of metabolic rate increase over geological time relative to a calculation assuming constant temperature (figure 4*a*). Unrealistically conservative assumptions that brachiopod and bivalve shells of similar dimension contain equivalent amounts of soft tissue and share equal temperature-adjusted per-gram metabolic rates also do not alter the magnitude or timing of the observed increase in metabolic rate (figure 4*b*). To address potential biases associated with uneven sampling of small species and specimens over geological time, we recalculated mean metabolic rates after excluding all taxa smaller than 10 mm in longest dimension. This treatment has negligible impact on the Phanerozoic

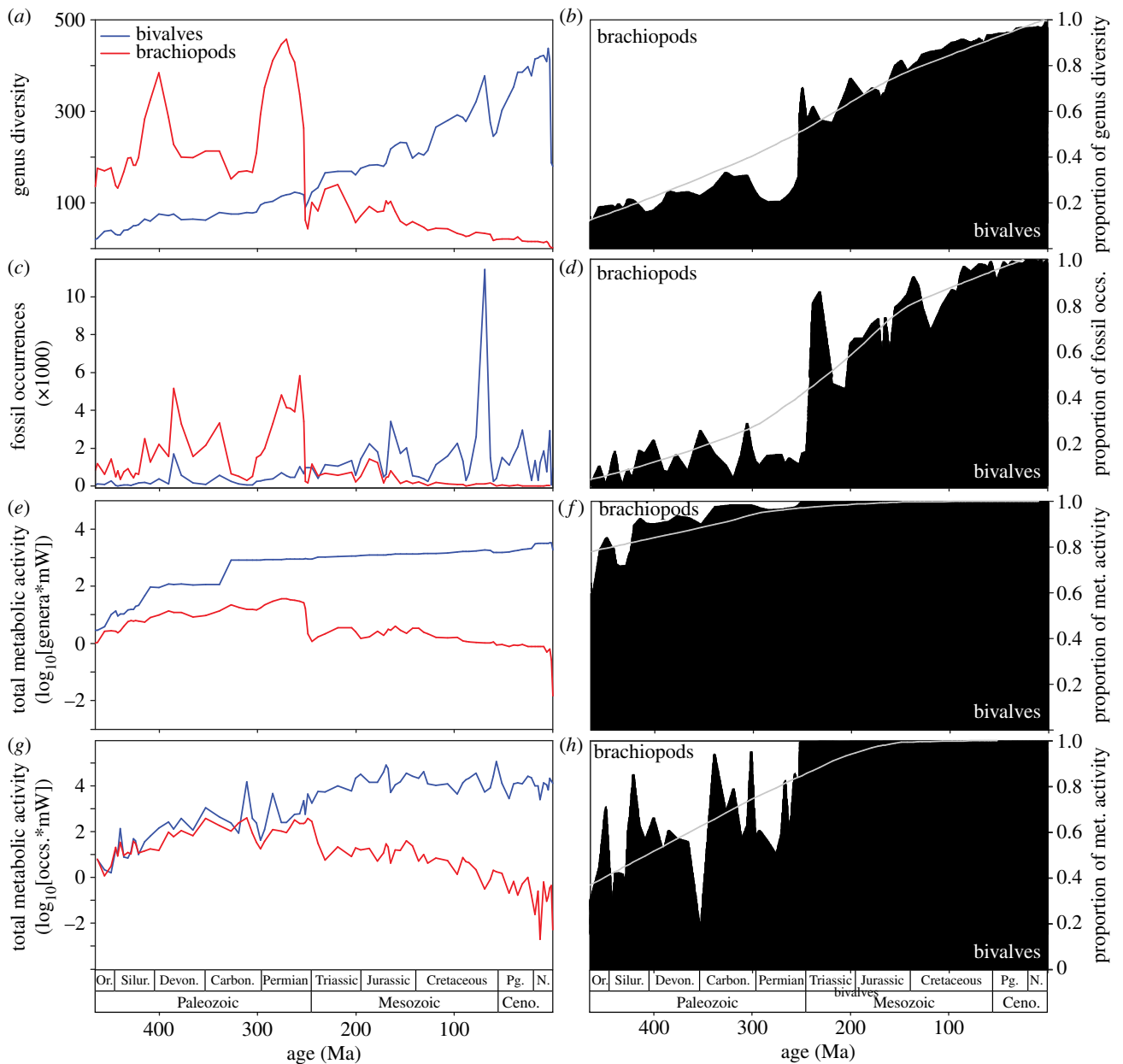


Figure 1. Trends in the absolute and proportional diversity, occurrence frequency and metabolic contribution of bivalves versus brachiopods over the past 465 Myr, illustrating that although bivalves constituted a small fraction of taxonomic diversity and fossil occurrences during the Palaeozoic (more than 250 Ma), they already accounted for more than half of all metabolic activity. (a,b) Genus diversity. (c,d) Occurrence frequency. (e,f) Total metabolic activity based on the per genus metric using range-through treatment of genera reported in the PaleoDB. (g,h) Total metabolic activity based on the per occurrence metric. Grey curves in b, d, f and h represent lowess fits to the proportional data. All increasing trends in proportional data are statistically significant based upon Spearman rank order correlation with time (b: $\rho = 0.97$, $p < 0.0001$; d: $\rho = 0.93$, $p < 0.0001$; f: $\rho = 0.98$, $p < 0.0001$; h: $\rho = 0.94$, $p < 0.0001$). (Online version in colour.)

trend in mean per taxon metabolic rate (figure 4c). Because the arithmetic mean of a strongly skewed distribution such as that analysed here can be sensitive to outliers, we reanalysed the data after excluding the largest 10% of fossil occurrences for each stage. This treatment of the data also does not change the direction or magnitude of the trend in metabolic rate (figure 4c).

The long-term increase in mean metabolic rate is controlled by both the consistently larger sizes of bivalves relative to brachiopods and the long-term trend towards a higher proportion of bivalves relative to brachiopods in terms of genera, occurrences and fossil specimens (figure 5). The mean shell size of bivalves has been consistently larger than that of brachiopods throughout the Phanerozoic, and so the trend towards greater proportional diversity and abundance of bivalves has caused a long-term shift towards larger overall mean size. Moreover, the

difference in mean size between bivalves and brachiopods has increased during post-Palaeozoic time owing to an increase in the mean size of bivalves, increasing the differences in mean metabolic rate between the two clades.

4. Discussion

Calculation of metabolic rates from the fossil records of brachiopod and bivalve reveals two key findings: (i) from a metabolic perspective, bivalves were at least as important as brachiopods in Palaeozoic oceans and (ii) the total metabolic activity of brachiopods and marine bivalves has increased enormously over Phanerozoic time owing to increases in the diversity, abundance and size of bivalves. These findings are not affected by uncertainty in the key parameters determining

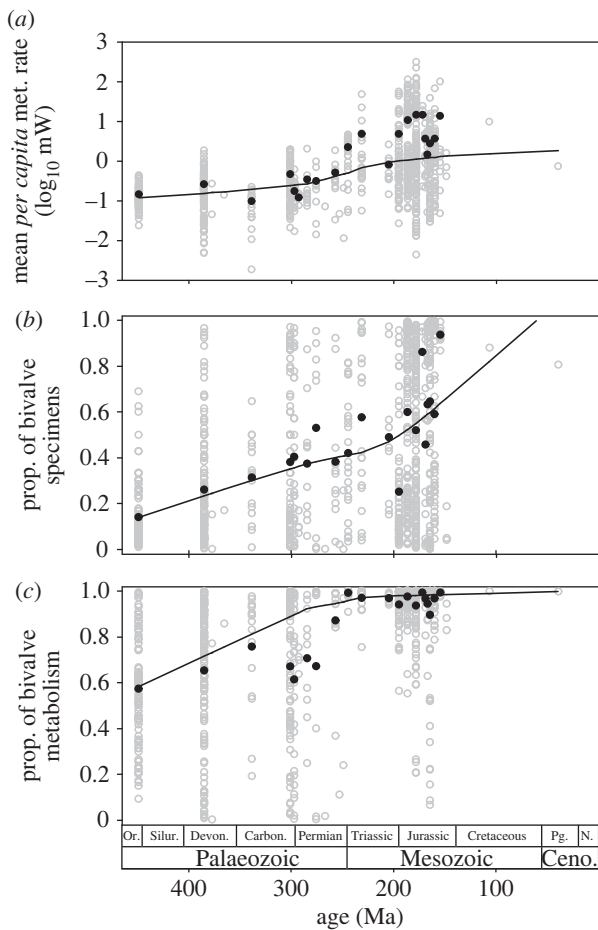


Figure 2. Trends in the contribution of bivalves to total specimens of both bivalves and brachiopods and metabolic activity within fossil assemblages containing both clades, illustrating the long-term increase in mean metabolic activity and the large proportional contribution of bivalves to individual collections even during Palaeozoic time. (a) Mean *per capita* metabolic rate. (b) Proportion of specimens accounted for by bivalves. (c) Proportion of metabolic activity accounted for by bivalves. Open grey circles—mean values for individual fossil collections. Filled black circles—mean values across collection means within a stage for stages represented by five or more collections. Black curves represent lowest fits to the data. All increasing trends are statistically significant based upon Spearman rank order correlation with time (a: $\rho = 0.49$, $p < 0.0001$; b: $\rho = 0.41$, $p < 0.0001$; c: $\rho = 0.59$, $p < 0.0001$).

metabolic rate, such as ambient temperature, scaling of shell length to tissue mass, taxon-specific scaling constants or the exclusion of bivalves that are not suspension feeders. These findings also appear unlikely to result from sampling biases. If anything, the Palaeozoic fossil record is biased against the preservation of bivalves owing to the early diagenetic dissolution of aragonite shells [42], whereas the post-Jurassic record may be biased against brachiopods owing to their reduced palaeoecological and biostratigraphic importance and consequent lack of researcher interest. Moreover, our data coverage for bivalves is poorer than that for brachiopods in both our primary and supplementary analyses. Correction for these biases might reduce the magnitude of increase in per genus and *per capita* metabolic rates over geological time, but it would not alter the basic finding that bivalves have been the metabolically dominant clade throughout the Phanerozoic. If anything, bivalve metabolic dominance in the Palaeozoic ocean may have been greater than our calculations indicate owing to the combined effects of diagenetic loss and relatively poorer coverage in our dataset. The wider variety

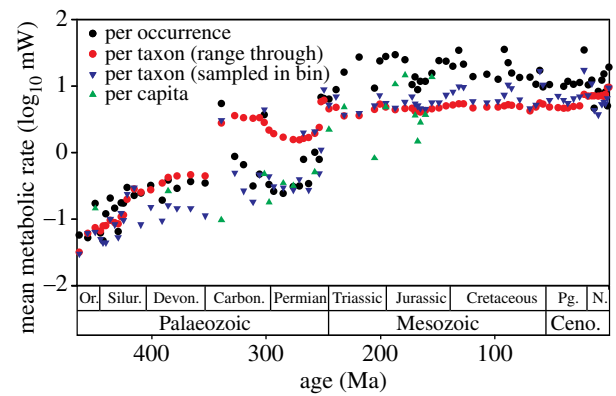


Figure 3. Comparison of mean per taxon, per occurrence and *per capita* metabolic rates of bivalves and brachiopods over the past 465 Myr, illustrating a long-term increase by nearly three orders of magnitude and close agreement across all metrics relative to change over time. Per taxon rates were calculated both using a range-through method (in which a genus is assumed to be present in all stages between its first and last known occurrences) and a sampled-in-bin method (in which a genus is only included in the calculation of the mean value when it has a known occurrence within a given stage). All increasing trends are statistically significant based upon Spearman rank order correlation with time (*per occurrence*: $\rho = 0.78$, $p < 0.0001$; *range-through Paleodb*: $\rho = 0.98$, $p < 0.0001$; *sampled in bin*: $\rho = 0.96$, $p < 0.0001$; *per capita*: $\rho = 0.84$, $p < 0.0001$). (Online version in colour.)

of feeding modes in bivalves versus brachiopods, including suspension feeding, sediment mining, deposit feeding, predation, chemosymbiosis and photosymbiosis [24], also does not account for their metabolic dominance. The vast majority of bivalves, like all brachiopods, are suspension feeders [24] and they alone account for as much metabolism as brachiopods during Palaeozoic time and the vast majority during post-Palaeozoic time (electronic supplementary material, figure S1).

Although the rise of bivalves may have been detrimental to brachiopods, the magnitude of the long-term increase in bivalve metabolism is too large to be attributed primarily to the displacement of brachiopods. By all metrics, bivalves account for the majority of metabolic activity during the Palaeozoic. Consequently, even complete displacement of brachiopods would result in less than a doubling of metabolic activity by bivalves. To offset the implied increase in total metabolic activity with a decrease in the density of individuals on the seafloor, the density of bivalves would need to have decreased by more than a factor of 100. This scenario is not plausible. If anything, the density and activity levels of bivalves and other animals on the seafloor appear to have increased over Phanerozoic time. Post-Palaeozoic bivalve shell beds are typically thicker than Palaeozoic brachiopod shell beds, whereas brachiopod shell beds have maintained similar thicknesses [43]; the bioturbation of marine sediments has become deeper and more extensive over Phanerozoic time [44]; and animal skeletons have become an increasingly important component of the sedimentary rock record [45,46]. Thus, our calculated hundred-fold increase in mean per genus, per occurrence and *per capita* metabolic rates may actually underestimate the magnitude of increase in the total metabolic activity of bivalves across the Phanerozoic, because it does not account for any associated increase in population density.

Unlike diversity data (cf. [6]), metabolic data are unambiguous in ruling out competition with brachiopods for food as the main factor underlying the rise of bivalves. Given the

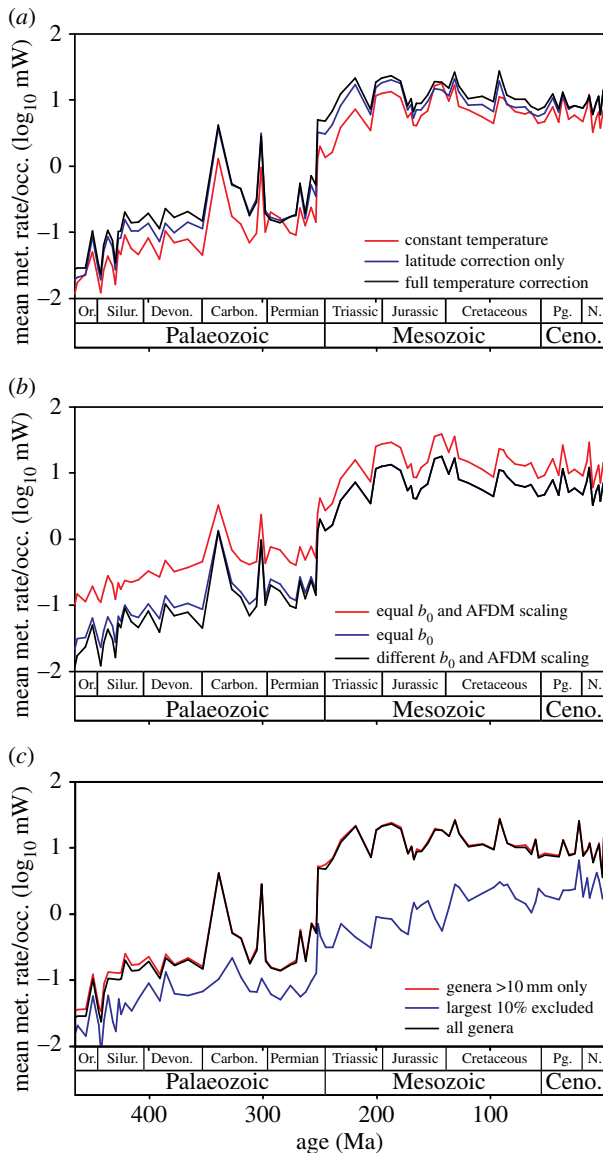


Figure 4. Sensitivity analysis showing that the increase in mean metabolic rate is unaffected by uncertainties related to temperature, the tissue mass and per gram metabolic rate of brachiopods and the extremes in the size distribution. Results presented here use the mean metabolic rate per occurrence because per genus rates cannot be made spatially explicit to account for temperature gradients and *per capita* rates are too sparse for the Cenozoic due to the rarity of brachiopods. (a) Influence of temperature on calculated metabolic rates. First, we assumed that all taxa experienced the same temperature (constant temperature: 15°C). Second, we assumed that global mean temperatures did not vary over geological time, but that a linear, 30°C temperature gradient (0–30°C) has always existed from the equator to the poles (latitude correction only). Third, we assumed that both global mean temperature has varied following the palaeoclimate reconstruction of Royer *et al.* [36] and there has always existed a temperature gradient of approximately 30°C from equator to pole (full temperature correction). (b) Influence of assumptions regarding soft tissue mass and b_0 values on trends in metabolic rates, illustrating the comparatively small effect of uncertainty in these parameters. The long-term increase in mean metabolic rate is indicated even under the unrealistically conservative assumptions that brachiopods and bivalves have the same scaling of shell length to AFDM and the same b_0 values. (c) Influence of small and large taxa on trends in metabolic rates. Mean metabolic rates are virtually unaffected by the exclusion of all genera less than 10 mm in maximum dimension. Mean metabolic rates are systematically lower when the largest 10% of occurrences are excluded from each stage, particularly during the Early Mesozoic, but the direction and magnitude of the Phanerozoic trend in mean metabolic rate is unaffected. (Online version in colour.)

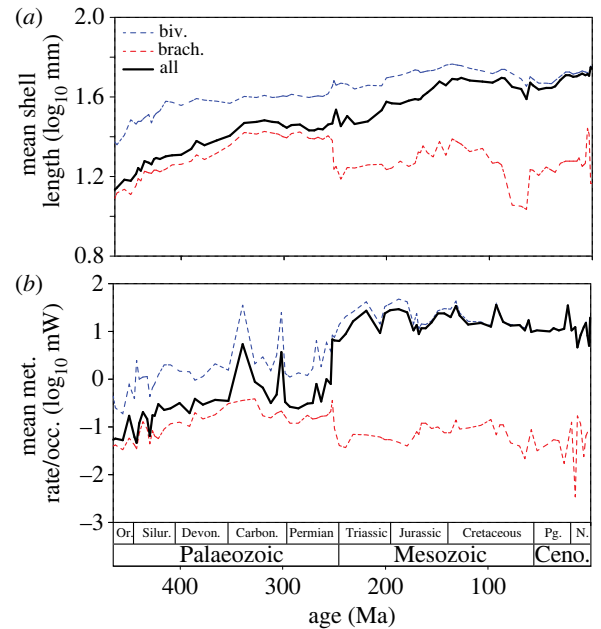


Figure 5. Trends in the mean sizes (a) and per occurrence metabolic rates (b) of bivalves and brachiopods over the past 465 Myr, illustrating that the long-term increase in overall metabolic rate is due to both the larger sizes of bivalves and their increase in proportional occurrence frequency towards this day, with an additional contribution from a long-term increase in mean bivalve size. Sizes are means across genera from the range-through treatment of the PaleoDB. Mean metabolic rates across genera following the per occurrence treatment with corrections for latitude and secular variation in global mean surface temperature. Increases in size over time are statistically significant across all genera ($\rho = 0.96$, $p < 0.0001$) and bivalves alone ($\rho = 0.86$, $p < 0.0001$) but not within brachiopods ($\rho = 0.13$, $p = 0.25$). Increases in per occurrence metabolic rate over time are statistically significant across all occurrences ($\rho = 0.78$, $p < 0.0001$) and bivalves alone ($\rho = 0.66$, $p < 0.0001$) but not within brachiopods ($\rho = -0.14$, $p = 0.19$). (Online version in colour.)

large increase in bivalve energy use as well as the small and decreasing magnitude of brachiopod energy use, most of the increase in bivalve metabolism must have occurred through the acquisition of resources that were never used by brachiopods. Rather than displacing brachiopods, the metabolic rise of bivalves occurred either at the expense of other clades or in response to an increase in the total amount of available food. If food availability has increased over geological time, as has been widely proposed [47–49], then brachiopods were apparently unable to capitalize on these additional resources. This scenario is consistent with previous suggestions that brachiopods were displaced from open shelf ecosystems by increases in predation intensity and bioturbation [50,51]. However, recent analyses of mass independent oxygen isotope fractionation in sulfate minerals suggest that gross primary production has not increased substantially over the past 350 Myr [52]. If accurate, this finding would imply that the metabolic rise of bivalves involved the displacement of other animals or microbes, rather than a response to a large increase in total food availability.

5. Conclusion

Metabolic data provide a new perspective on the evolutionary histories of bivalves and brachiopods. The metabolic

activities of marine bivalves have increased by more than two orders of magnitude over the past 465 Myr. The vast majority of this increase occurred via the acquisition of new resources rather than by displacement of brachiopods. Moreover, the canonical view of a Permian–Triassic transition from brachiopod to bivalve dominance [5–7] is a product of historical focus on taxonomic diversity and numerical abundance as measures of biological success. From a metabolic perspective, the oceans have always belonged to the clams.

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