

QUANTIFYING SEAFOOD THROUGH TIME: COUNTING CALORIES IN THE FOSSIL RECORD

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ABSTRACT.—Energy and nutrients are the fundamental currencies of ecology and changes in energy and nutrient availability are thought to have played an important role in the long-term development of marine ecosystems. However, meaningfully quantifying when, where, and how such changes have occurred has been a difficult and longstanding problem. Here, some of the various lines of evidence that have been brought to bear on this issue in the past two decades are reviewed, particularly those based on the fossil record of benthic invertebrates. This paper focuses on abundance, body size, and metabolism, three distinct but closely interrelated aspects of ecosystem structure that control (or are controlled by) energy fluxes. Each of these is subject to biases and inherent uncertainties that present significant challenges for making inferences from the fossil record, but when carefully controlling for environmental, taphonomic, and methodological variations there are robust trends that can be discerned above the noise. Integrating these different types of data in a single quantitative framework presents additional complications, but coherent patterns emerge from some such analyses. Accurate quantification of energetic trends in the fossil record is difficult but is a worthwhile goal because of its potential to illuminate the energetic dimension of major diversifications, extinctions, and secular ecological-evolutionary trends and link them more directly to their Earth Systems context.

INTRODUCTION

In 1993, Richard Bambach published a paper in Paleobiology entitled *Seafood through time—changes in biomass, energetics, and productivity in the marine ecosystem* (Bambach, 1993). In this and subsequent papers (Bambach, 1993, 1999; Bambach et al., 2002; Bambach and White, 2002; Bush and Bambach, 2011), Bambach and colleagues assembled multiple lines of evidence to argue that: 1) the standing biomass and the energy budgets of marine animal ecosystems had increased in steps over the course of the Phanerozoic; 2) these steps had been facilitated by increases in marine primary productivity; and 3) productivity increases were, in turn, linked to expansions of terrestrial ecosystems via their effects on continental weathering and nutrient runoff. Along with papers and books by Geerat Vermeij (1977, 1987, 1995, 2002, 2004) who also argued for stepwise increases in productivity and energetics, but thought that these increases were related to volcanism and seafloor spreading (Vermeij, 1995), these papers drew attention to

conspicuous but poorly defined long-term trends in the ecological structure of marine fossil assemblages. Equally importantly, they refocused the ongoing debate about Phanerozoic diversity by reemphasizing the Earth Systems-focused perspective of Valentine, Tappan, and others (Valentine and Moores, 1970; Valentine, 1971, 1973; Tappan, 1982, 1986), and framing diversity trends in terms of the fundamental ecological currencies of energy and nutrients.

Given the limitations of the available data at the time, Bambach's arguments in 1993 were necessarily non-quantitative. He wrote that, "While anecdotal and descriptive, the paper cites unambiguous and robust patterns. On the global scale considered here, an effort at quantification would be too speculative at this time." (Bambach, 1993, p. 372). Two decades later, quantifying energetic trends remains a major challenge for paleoecology, and the difficulty of this problem largely accounts for the fact that, although frequently cited, the hypotheses posed by Bambach and Vermeij have been tested only rarely.

Over the past two decades, enormous quantities of data have been gathered and assembled into databases. Interest in fossil abundance patterns has grown, both for their relevance to explicitly paleoecological questions (McKinney et al., 1998; Lupia et al., 1999; Peters, 2004; Finnegan and Droser, 2005; Clapham et al., 2006; Hull et al., 2011) and in recognition of the need to sample-standardize local (alpha) diversity estimates (e.g., Adrain et al., 2000; Peters, 2006). Inclusion of quantitative abundance data in occurrence-based databases such as the Paleobiology Database (Alroy et al., 2008) offers a far richer picture of the fabric of the fossil record than was available in 1993, especially when combined with stratigraphic databases (Peters, 2005). There has also been a surge of interest in evolutionary body size trends, and many size measurements of specimens from field censuses, museum collections, and published monographs are now available (Kosnik, 2005; Payne, 2005; Hunt and Roy, 2006; Kosnik et al., 2006; Payne et al., 2009, 2012; Rego et al., 2012). In neontology, the development of the macroecological paradigm (Brown and Maurer, 1989; Brown, 1995; Witman and Roy, 2009) and the Metabolic Theory of Ecology (MTE; Gillooly et al., 2001; Allen et al., 2002; Enquist et al., 2003; Brown et al., 2004; Savage et al., 2004b) have spurred research focused on quantifying energetic patterns across different taxa, ecosystems, and scales. Spurred by concerns about anthropogenic effects on marine ecosystems, marine ecological research has greatly expanded knowledge of the metabolic physiology and population ecology of extant marine invertebrates (Brey, 2001). An ongoing renaissance in the development and application of stable isotope and other geochemical proxies has also greatly refined our ability to reconstruct climate and environment in deep time. Summarizing this literature is beyond the scope of this paper, but useful recent reviews include Ivany and Huber (2012; various climate proxies), Katz et al. (2010; various foraminiferan-based proxies), Schouten et al. (2013; lipid biomarkers), Brocks and Pearson (2005; deep-time biomarkers), Paytan (2009; paleoproductivity proxies) and Tribouillard et al. (2006; paleoproductivity and paleoredox proxies).

It is now feasible to at least outline a quantitative framework for examining energetic pattern in greater environmental and temporal detail. Determining when, where, and how the

distribution of marine biomass and associated energy fluxes has changed throughout the Phanerozoic is important for several reasons. Gradients in energy and nutrient availability play a conspicuous role in controlling the distribution of diversity and standing biomass in the modern oceans (Rex et al., 2005, 2006; Belanger et al., 2012), and have likely done so throughout Earth history. Evolutionary events and trends may ultimately be driven by physical forcings or biological competition, but they are proximally determined by the differential flow of energy and nutrients through individuals and populations (Van Valen, 1976). Changes in both marine and terrestrial primary productivity have been hypothesized to be major factors in driving Phanerozoic marine evolutionary and diversity trends (Tappan, 1982, 1986; Bambach, 1993, 1999; Vermeij, 1995, 2002, 2004; Martin, 1996, 2003; Falkowski et al., 2004) and are thought to play an important role in several mass extinctions (see van de Schootbrugge and Gollner, 2013; Hull and Darroch, 2013), but evolutionary patterns cannot be confidently linked to productivity trends without information about the spatial and environmental distribution of individuals and biomass through time.

Similarly, direct or diffuse competitive interactions have been invoked to explain the differential macroevolutionary success of clades through time (see discussion in Sepkoski, 1996), but, to the extent that they occur, such interactions ultimately are about the division of energy and nutrient resources among individuals and populations. Consequently, putative cases of clade competition cannot be properly evaluated without data regarding the absolute (as opposed to relative) abundance, biomass, or metabolic activity of the groups in question across environments and through time (Finnegan and Droser, 2005, 2008).

This paper discusses work, mostly from the past two decades, that has sharpened understanding of the timing and magnitude of biomass and energetic trends. To limit the scope of the discussion, the focus herein is on the Phanerozoic record of benthic invertebrates in level-bottom, shallow to deep subtidal platform and shelf environments. These depositional environments are by far the best represented in the stratigraphic record and, other than reefs, vents, and seeps, host the highest concentrations of benthic macrofaunal biomass in the modern oceans (Wei et al., 2010). Due to nutrient delivery

from continental runoff, shelf-marginal upwelling, and the relatively high proportion of primary productivity that is exported to the seafloor, these probably have been the most consistently productive benthic marine environments throughout Earth history. In the modern ocean, these environments account for only 6% of the seafloor area, but contain an estimated 21% of global benthic biomass (Wei et al., 2012).

Colonization of the deep sea (Smith and Stockley, 2005) or the development of planktonic pelagic ecosystems (Falkowski et al., 2004) are not discussed herein. These represent enormous expansions of global marine biomass, but the pre-Mesozoic fossil record of deep sea macrofauna is fragmentary and poorly known, while pelagic productivity trends are reviewed elsewhere in this volume (see van de Schootbrugge and Gollner, 2013; Hull and Darroch, 2013). The goal of this paper is to review the evidence for long-term changes within a single (albeit very broadly defined) habitat.

This paper focuses on three types of evidence that are distinct but interrelated: abundance and biomass, body size, and metabolism. Following Bambach (1993), long-term trends are the primary focus, although shorter-term patterns associated with some mass extinctions are also reviewed. Ways in which abundance, body size, and metabolic data can be integrated utilizing simple ecological and physiological principles to produce approximate estimates of individual, per-taxon, and paleocommunity respiration rates are discussed. The approach outlined herein is crude in that it treats assemblages of fossils as directly comparable to living populations despite the well-known distortions of population and community structure introduced by taphonomy and time-averaging. More sophisticated analyses that account for other aspects of energy budgets such as growth and reproduction and that integrate over the lifespan of an entire individual are possible and have been attempted for some paleocommunities (Powell and Stanton, 1985), but require additional parameters that are difficult to estimate confidently for many extinct taxa. Whether this approach is sufficient to discern original environmental and temporal community energetic gradients depends on the signal-to-noise ratio—the magnitude of the original gradients relative to the magnitude of the noise introduced by the combined effects of taphonomic distortion and analytical simplification. Some of the major factors influencing this ratio are discussed, and

sensitivity tests for evaluating trends in the fossil record and for comparing fossil estimates with respiration data from modern benthic assemblages are suggested.

BENTHIC ABUNDANCE AND BIOMASS

As background for considering temporal trends, it is helpful to briefly discuss the geographic, environmental, and bathymetric distribution of benthic abundance and biomass in the modern oceans. This reveals something about the physical factors that exert the most influence on the distribution of individuals and biomass, and therefore, which Earth systems changes might be expected to have had an influence on standing stocks of abundance and biomass over geological timescales. It also serves to highlight the range of values apparent in a single geological instant—variation that must be taken into account when attempting to delineate temporal trends. Wei et al. (2010) added shallow-water (< 200 m) data to the deep-sea benthic biomass and abundance dataset compiled by Rex et al. (2006), and used a random forest model trained on the relationship between these data and a suite of physical predictors including depth, temperature, and various metrics of primary production to predict the global distribution of standing stocks of benthic abundance and biomass across four size classes. This analysis highlighted several important patterns. Whereas bacterial biomass exhibited remarkably little variation with depth or latitude, the standing biomass of invertebrate macrofauna and megafauna (individuals retained by a 520 μm mesh and larger, the size classes most commonly studied in the fossil record) decreased sharply with depth and distance from land and increased with latitude, exhibiting minima in the central abyssal plains and maxima on mid- to high-latitude continental shelves (Fig. 1A, B). Controls on the global distribution of benthic invertebrate biomass are complex, but this and other analyses (Rex et al., 2006; Johnson et al., 2007; Ruhl et al., 2008; McClain et al., 2012; Wei et al., 2012) suggest that pelagic-benthic coupling can be strong and that important roles are played by:

- 1) depth and its numerous physical correlates because the proportion of net primary production (NPP) that is exported to benthic ecosystems decreases with depth (Lutz et al., 2007);
- 2) primary productivity in surface waters, which tends to influence the intercept but not the slope of the depth-NPP export relationship;
- 3) distance

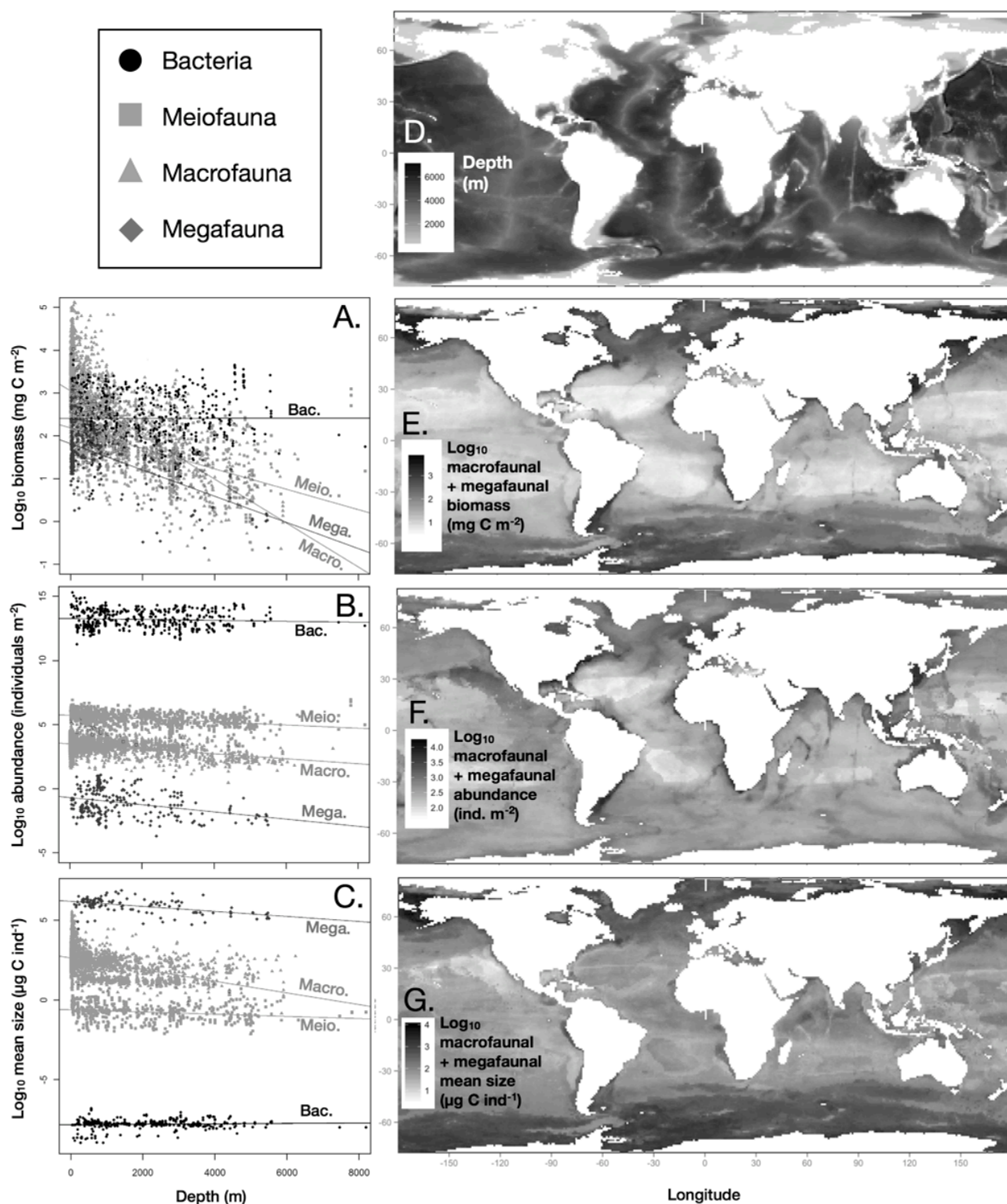


FIGURE 1.—A–C) Global relationship between depth and: A) sampled biomass; B) abundance; and C) mean body size of benthic organisms in four size classes, modified from Wei et al. (2010). Relationships with latitude and longitude have been removed by partial regression. D–G) D) shows global bathymetry and the predicted geographic distribution of: E) biomass; F) abundance; and G) mean body size of invertebrate macrofauna + megafauna from a random forest model trained on the relationship between the samples in A–C and a suite of physical variables including depth, temperature, and primary productivity. D–G produced from Files S2 and S3 in Wei et al. (2010).

from land because this tends to reduce nutrient delivery from both continental runoff and shelf-marginal upwelling; 4) latitude, possibly because of the comparatively short food chains and weak microbial loops at high latitude (Kirchman et al., 2009) and the effects of water temperature on microbial remineralization rates, the efficiency of NPP export to benthic habitats, and the residence time of organic carbon on the seafloor (Laws et al., 2000; Ruhl et al., 2008). Hotspots of elevated macrofaunal biomass associated with many submarine canyons (De Leo et al., 2010) also reinforce the importance of terrigenous detrital inputs, a point emphasized by Bambach (1993, 1999).

Notably, variation in the distribution of macrofaunal and megafaunal biomass appears to be more strongly controlled by bathymetric (Kaariainen and Bett, 2006) and latitudinal (Moran and Woods, 2012) gradients in mean body size (Fig. 1C,G) than by gradients in the abundance of individuals (Fig. 1B,E,F), particularly in the shelf to slope environments that are best represented in the fossil record. Body size patterns will be discussed in more detail after a review of the evidence for temporal trends in biomass and abundance below.

Temporal trends in the fossil record

Indirect evidence for a Phanerozoic increase in the standing biomass of benthic ecosystems from trends in diversity, paleocommunity structure, and ecospace filling has been reviewed most recently by Bush and Bambach (2011), and is only briefly summarized here. The diversity of skeletonized marine animals has increased substantially since the Cambrian both globally (Sepkoski, 2002; Alroy et al., 2008) and locally (Bambach, 1977; Bush et al., 2004, 2007)—a trend that implies a correlative increase in standing abundance and biomass. Proportions of predatory and motile genera also have risen sharply through time in multiple skeletonized groups, a trend that would be difficult to support energetically without commensurate increases either in primary productivity and the biomass of prey species, or in prey specificity (Valentine, 1971) or consumption efficiency (Payne and Finnegan, 2006) of predators. The distribution of taxa in ecospace provides important constraints on biomass, but relationships between diversity and abundance patterns are extremely complex and poorly understood, and it is impossible to derive quantitative biomass estimates from

diversity data alone. Although the data are scarce and often harder to quantify and interpret, there are several direct lines of evidence for an overall increase in benthic biomass through the Phanerozoic.

Unfossiliferous versus fossiliferous sediments

A very coarse measure of the spatiotemporal distribution of fossil content can be obtained by comparing the distributions of fossiliferous and unfossiliferous sedimentary rocks. Peters (2007) and Peters and Heim (2010) presented evidence for a long-term (although not obviously stepwise) Phanerozoic decline in the proportion of unfossiliferous marine sedimentary rocks. Peters (2007) attributed this trend to the prevalence of at least episodically hypoxic conditions in epeiric depositional environments, which were much more widespread in the Paleozoic than in the post-Paleozoic. Smith and McGowan (2008) observed a similar trend in Europe (Fig. 2), but suggested that the trend instead reflects an expanding biosphere in which the abundance of animals has gradually increased through time due to increases in primary productivity and nutrient levels (Martin, 2003). The coarse bivariate

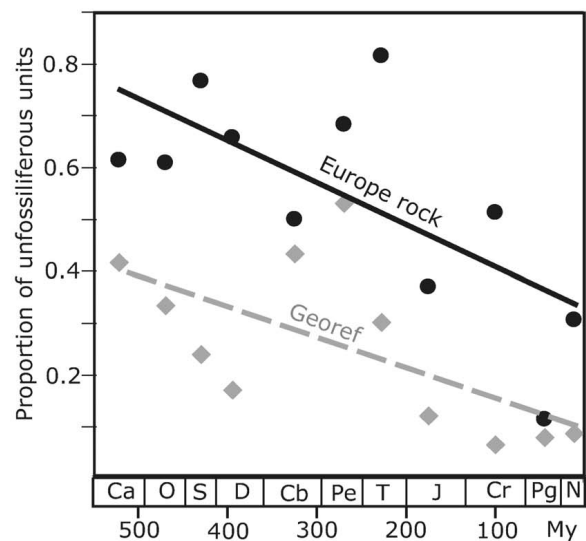


FIGURE 2.—Proportions of marine stratigraphic units that contain no recorded fossils. Black circles and regression lines based on a survey of European rock units by Smith and McGowan (2008); gray diamonds and regression line based on a GeoRef search by Peters (2007). Reproduced with permission from Smith and McGowan (2008).

binning scheme employed by these three studies (fossiliferous versus unfossiliferous stratigraphic units) does not allow resolution of subtle trends in fossil concentration, which would help to differentiate between these two models. The epeiric seaway hypothesis predicts that the abundance of fossils has remained relatively constant through time within different depositional environments, and that the long-term decrease in the proportion of unfossiliferous units is explained by a decrease in the area of epeiric seaways. In contrast, the expanding biosphere hypothesis predicts that the abundance of fossils has approximately tracked global diversity trends through time across a range of depositional environments (Smith and McGowan, 2008). Differentiating between these two models, which have very different implications for Phanerozoic trends in paleocommunity energetics, should be facilitated by increasing integration of stratigraphic and paleobiological databases (e.g., Heim and Peters, 2010; Peters and Heim, 2010; Finnegan et al., 2012).

Bioturbation intensity

Trends in the depth and extent of bioturbation (ichnofabric) reflect infaunal activity through time. Ichnofabric development is influenced by both abundance and per-capita activity level and therefore cannot be interpreted solely in terms of biomass density, but it is particularly valuable because it is the only direct record of many nonskeletonized burrowing taxa (Thayer, 1983). Initial appearance of bioturbated sediments in the late Ediacaran–lower Cambrian (Seilacher and Einsele, 1982; Bottjer et al., 2000) was followed by increases in mean bioturbation intensity across a range of deposition environments during both the Cambrian and Ordovician biodiversifications (Droser and Bottjer, 1988, 1989, 1993; Mangano and Droser, 2004). In the wake of the Permo–Triassic mass extinction, bioturbation was markedly reduced in many Early Triassic depositional environments and did not return to pre-extinction levels until the Middle Triassic (Schubert and Bottjer, 1995; Pruss and Bottjer, 2004; Pruss et al., 2004). The subsequent Mesozoic–Cenozoic diversification of burrowing taxa in several groups and the appearance of new trace fossil types strongly imply a major increase in bioturbation (Thayer, 1983; Vermeij, 1987). There have been no field studies of long-term Mesozoic–Cenozoic ichnofabric trends, but an increase in bioturbation intensity over this interval

is suggested by—among other things—trends in the thickness of preserved storm beds (Brandt, 1986; Sepkoski et al., 1991).

Absolute abundance: shell beds and bioclastic fabrics

Fossil abundance data are critical for evaluating the ecological context of diversity trends (Peters, 2004; Clapham et al., 2006; Hull et al., 2011) and for discerning trends in paleocommunity structure and function (Wagner et al., 2006; Bush et al., 2007; Novack-Gottshall, 2007), but most quantitative abundance counts are collected without an accompanying measure of the sediment volume processed (or, in the case of quadrat counts, the bedding-plane area censused). Consequently, they can only measure the abundances of different bioclast producers as a proportion of the total count (relative abundance). Normalizing abundance to the number of individuals or fragments counted rather than to the amount of sediment processed forces the abundances of different groups to appear inversely correlated even if their absolute abundance trajectories are entirely independent of one another (Fig. 3; Aitchison, 1982; Grayson, 1984; Finnegan and Droser, 2005). Thus, relative abundance data are problematic because they can create the impression of zero-sum competitive ecological dynamics where none may have existed, and they cannot provide information about trends in the absolute abundance of fossils.

Absolute abundance data are more difficult to collect, especially in lithified sediments, and when available, they are difficult to interpret purely in terms of biological inputs. Concentrations of skeletal material in marine sediments are determined by a complex interplay of numerous factors including biological production and mortality rates, sedimentation and reworking rates, and rates of dissolution and fragmentation (Kidwell, 1986; Kidwell et al., 1986; Davies et al., 1989). At the outcrop scale, bed-to-bed variations in bioclastic concentration typically are controlled by processes such as event burial, storm winnowing and reworking, condensation, dissolution, and bioturbation. This physical overprinting adds considerable noise to the original signal of skeletal input. Even within a relatively homogeneous sedimentary environment, the controls on local fossil concentration can be complex and nonlinear (Finnegan and Droser, 2005; Tomašových and Schlögl, 2008). Nevertheless, fossil concentration

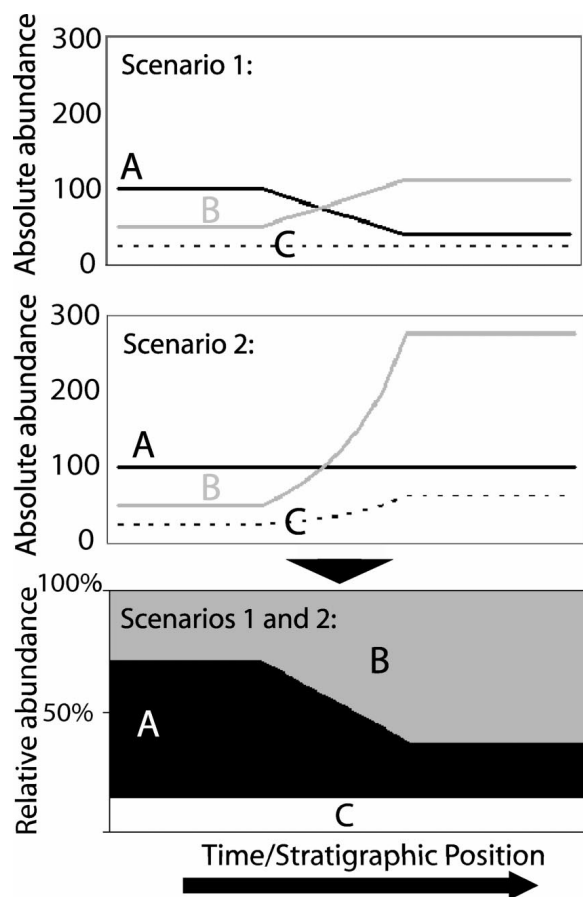


FIGURE 3.—Two hypothetical sets of absolute abundance trajectories that produce identical relative abundance trends. In Scenario 1, a decline in the relative abundance of taxon A results from a decrease in its absolute abundance. In Scenario 2, the decline is an artifact of normalization and is driven by increases in the absolute abundances of taxa B and C. Reproduced with permission from Finnegan and Droser (2005).

data are necessary for constraining long-term changes in benthic biomass, and, by controlling for variations in sedimentary environment and systematically censusing and averaging across many beds, it may be possible to extract a signal, however noisy, of long-term trends in skeletal production rate.

Although only a handful of such studies have been conducted, they have been informative. Li and Droser (1997, 1999) demonstrated that the frequency and the mean thickness of shell beds in carbonates of the Basin and Range region of the western US increased through the Cambrian and across the Early–Middle Ordovician boundary, suggesting that increases in diversity and infaunal

activity over this interval were accompanied by substantially increased skeletal production rates. This general trend is supported by point counts of thin sections and tabulations of bioclastic units in measured sections from Cambrian–Ordovician strata in Utah and Newfoundland (Pruss et al., 2010; Fig. 4), implying that it is a general trend at least in Laurentian carbonate shelf and slope environments. Fewer data are available to evaluate post-Ordovician trends in bioclastic abundance, but Kidwell and Brechley (1994, 1996) demonstrated that the proportional frequency distribution of Jurassic shell beds is more right-skewed (more thick beds) than that of Ordovician–Silurian shell beds, and that Neogene shell beds tend to be considerably thicker than Jurassic shell beds (Fig. 5). Known trends in skeletal mineralogy and taphonomy (e.g.,

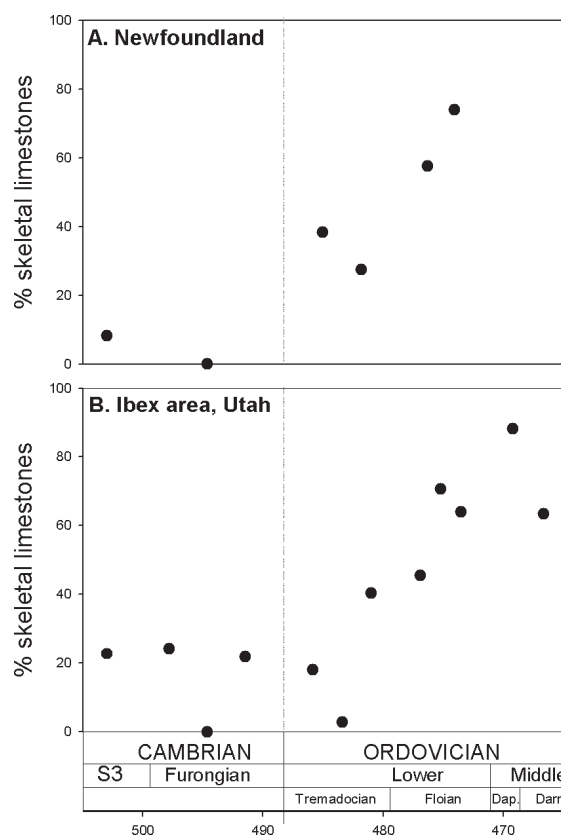


FIGURE 4.—Proportions of stratigraphic units (formations or members) logged as skeletal limestone (fossil wackestones, packstones, or grainstones), plotted against age in measured sections from A) Newfoundland (S. Pruss, field notes, 2005–2006); B) western Utah (S. Finnegan field notes, 2000–2005, and from Hintze, 1973); S3 = Series 3; Dap. = Dapingian; Dar. = Darriwilian. Reproduced with permission from Pruss et al. (2010).

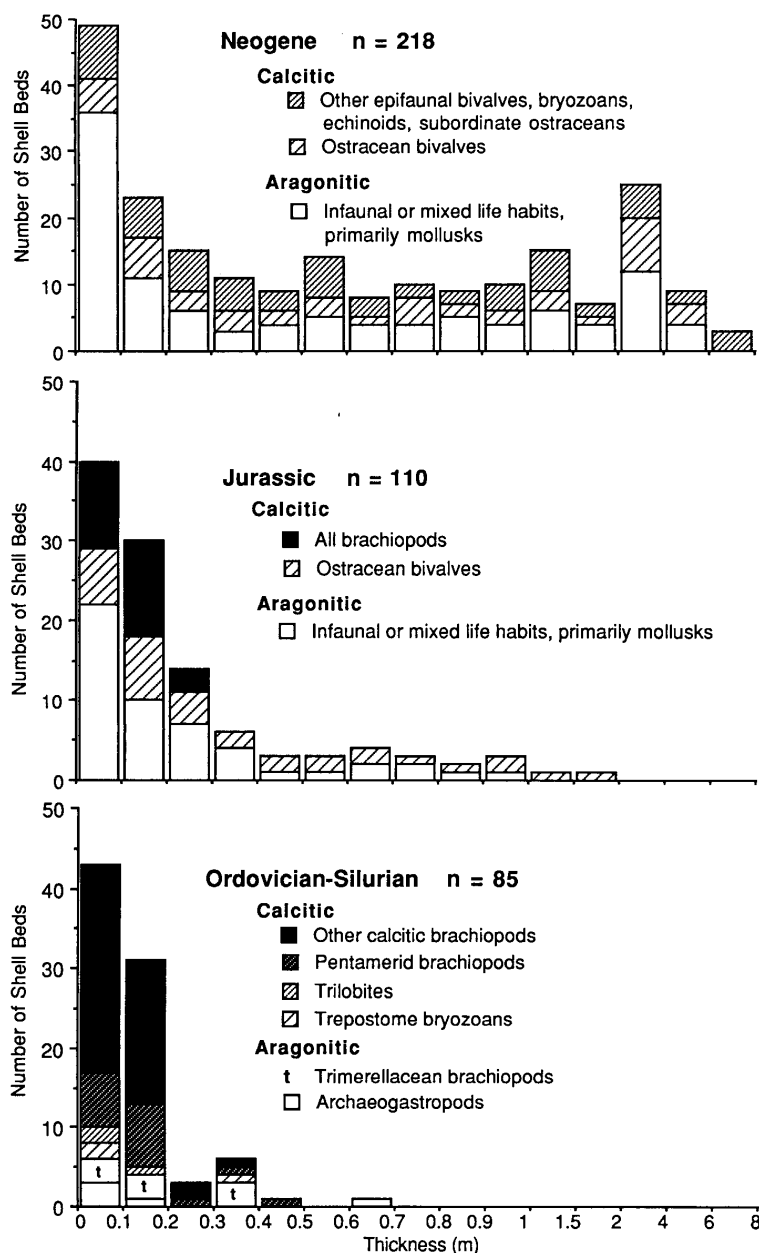


FIGURE 5.—Phanerozoic trend in the thickness frequency distribution and taxonomic composition of shell beds, reproduced with permission from Kidwell and Brenchley (1994).

Kowalewski et al., 1998; Oji et al., 2003) cannot easily explain this trend; hence, the most parsimonious explanation is a combination of increased durability and increased skeletal production rates (Kidwell and Brenchley, 1994, 1996).

Clear changes in bioclast abundance are also associated with at least some major mass extinction events (see also van de Schootbrugge and Gollner, 2013; Hull and Darroch, 2013). In a study of more than 600 hand samples and thin

sections from a late Permian–Early Triassic carbonate platform, Payne et al. (2006) showed that multiple facies record order-of magnitude declines in the volumetric contribution of animal bioclasts across the Permian–Triassic (P–T) boundary. Animal bioclastic contributions to carbonate production remained low throughout the Early Triassic, and had not fully returned to pre-extinction levels even by the early Middle Triassic (Payne et al., 2006). Taken together with the similar Permian–Triassic trend in bioturbation

intensity (Schubert and Bottjer, 1995; Pruss and Bottjer, 2004; Pruss et al., 2004), the decrease implies that the benthic biomass of animals was very low for a substantial period of time following the extinction.

The Early Triassic example highlights another important strength of biomass data. Diversity may take millions of years to fully recover following a major mass extinction simply because origination of new taxa takes considerable time—a lag does not necessarily imply ongoing environmental disruption (Kirchner and Weil, 2000; but see Lu et al., 2006). However, on geological timescales, benthic biomass should respond essentially instantaneously to changes in energy and nutrient availability. Indeed, the relatively few benthic taxa that do proliferate in the Early Triassic are mainly generalist ‘disaster’ taxa (Schubert and Bottjer, 1995; Rodland and Bottjer, 2001). Given this, the protracted interval of low bioclastic abundance implies either that primary production was generally low or that other environmental conditions prevented animal populations from fully exploiting available nutrient and energy resources (Payne et al., 2004, 2006; Ramezani et al., 2006; Sun et al., 2012). Comparable studies of other major mass extinction events are needed to determine the degree to which benthic biomass trends track trends in diversity or in environmental proxy data across different depositional environments and through time (see Hull et al., 2011; Hull and Darroch, 2013, for pelagic examples).

BODY SIZE AND BODY MASS

The data summarized above imply a long-term increase in benthic biomass, although they offer only the coarsest outline of timing and magnitude of increase. Thus far, this review has treated biomass and absolute abundance in the fossil record as largely synonymous, but the biomass of a given taxon per unit area is a function of both its population density and its mean body size. As previously noted, global-scale gradients in the modern distribution of benthic macrofaunal biomass largely reflect the influence of mean size rather than of abundance (Fig. 1). Broad bathymetric gradients in mean individual size have been recognized for some time, and are thought to be related to decrease in the availability of energy and nutrients from surface productivity with increasing depth and distance from productive coastal waters (Rex et al., 2006).

Latitudinal gradients in mean individual size have also been recognized, but are less pronounced (Fig 1C, G) and their causes less well understood. Despite much study of interspecific body-size gradients within marine invertebrate groups (Roy et al., 2000; Roy, 2002; McClain, 2004; Kaariainen and Bett, 2006; McClain et al., 2006; Berke et al., 2013) broadly generalizable macroecological patterns of interspecific size variation are not apparent (Berke et al., 2013), implying that mean size trends primarily reflect intraspecific size clines and changes in species-abundance structure rather than interspecific size trends.

Regardless of the mechanisms that give rise to body-size gradients, body size is a crucial parameter for any consideration of long-term trends in ecosystem energetics because it is strongly correlated with individual metabolic rate (Gillooly et al., 2001; West, 2002; Glazier, 2005; Seibel and Drazen, 2007; see discussion below). Trophic level is also closely related to individual body size in marine ecosystems (Jennings et al., 2001; Kerr et al., 2001; Shurin et al., 2006), but due to the enormous ontogenetic size range spanned by most marine benthic species, there may be only a weak relationship between mean adult body size and trophic level (Jennings et al., 2001; Shurin et al., 2006), particularly given that the majority of benthic invertebrate species are suspension or deposit feeders.

Because individual metabolic rate scales positively with body size, body size also constrains population density and local abundance (Damuth, 1991; Kerr et al., 2001; Marquet et al., 2005). On average, big animals tend to be less common than small animals, although the form of this relationship and its dependence on sampling, spatial scale, environment, and taxonomic group is controversial, and it may not always be apparent in local benthic communities (Warwick and Clarke, 1996; Dinmore and Jennings, 2004). In principle, it is possible for an overall Phanerozoic increase in absolute abundance to have been offset by compensatory reductions in mean body size such that total benthic energy budgets were unchanged. However, Phanerozoic trends in body size distribution (Kosnik et al., 2011) provide little support for this hypothesis.

Renewed interest in the evolutionary and ecological meaning of body size over the past decade has greatly increased the amount and the phylogenetic diversity of available fossil body-size data. Although there is much variation in how

body size is measured in the literature, different size metrics tend to be very strongly correlated with one another and even simple, one-dimensional size metrics capture most variation (Kosnik et al., 2006; Novack-Gottshall, 2008a). A full review of the current state of knowledge of body size trends in marine invertebrate groups would run to many pages and is beyond the scope of this paper, but some general trends can be highlighted.

Maximum size of marine animals

The maximum known size of marine animals has increased by about three orders of magnitude from the lower Cambrian to the Recent (Payne et al., 2009). Most of this increase occurred during the early Paleozoic, although within-clade maximum size trajectories show considerable variation (Payne et al., 2009). Maximum size is a useful measure of evolutionary potential (Bonner, 2006), and may provide information about environmental boundary conditions such as oxygen availability (Cloud, 1972), a potential explanation for the early Paleozoic increase in maximum size (Payne et al., 2009, 2011; Dahl et al., 2010; but see Butterfield, 2011). In principle, maximum size is also constrained by primary productivity and the length and complexity of food chains (Kerr et al., 2001), but the relationship between productivity and maximum size is not well understood. For making inferences about productivity and energy availability, measures of variance and central tendency are more informative, especially when combined with relative or absolute abundance data (Rex et al., 2006; Finnegan et al., 2011; McClain et al., 2012).

Size trends within clades

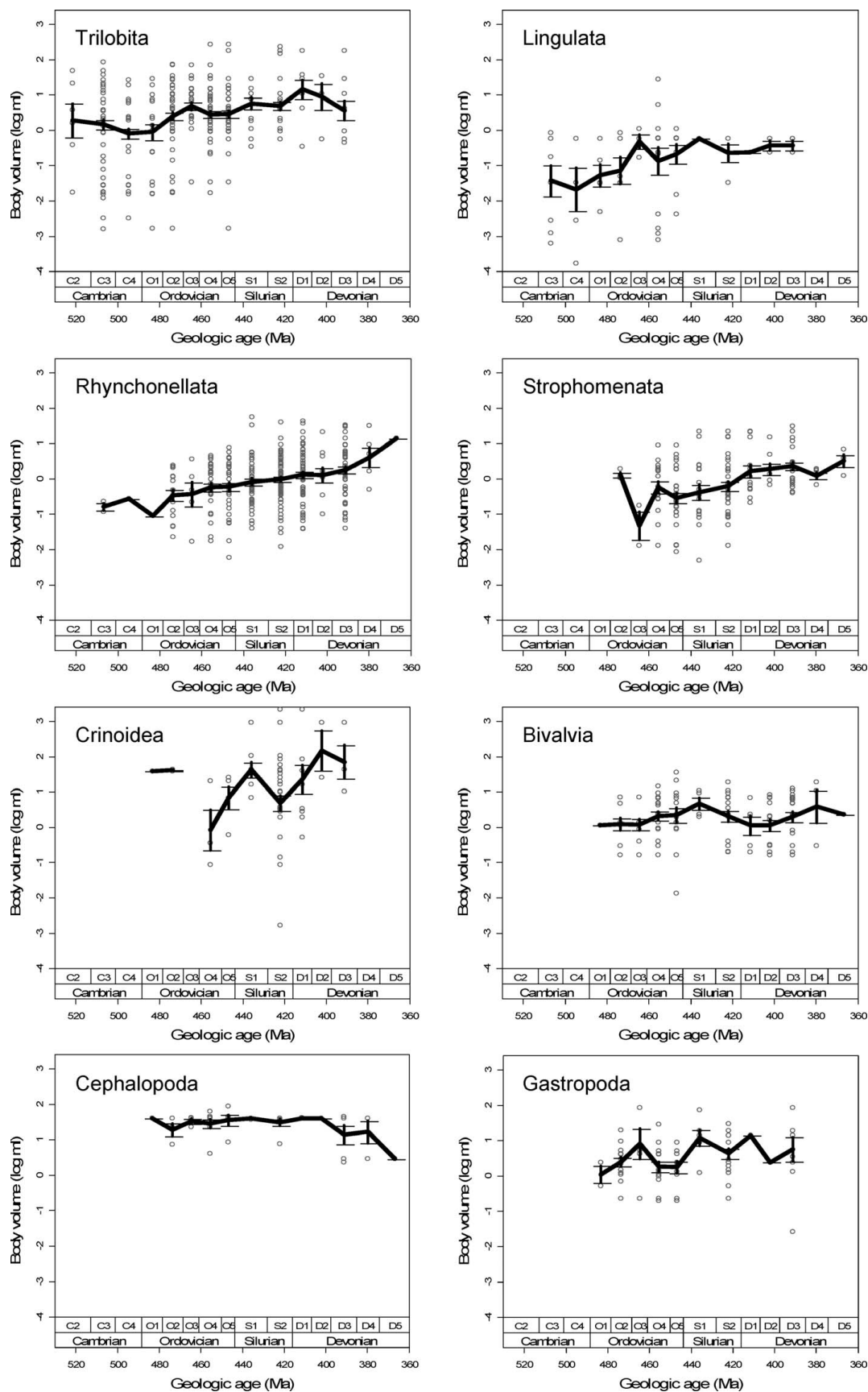
Novack-Gottshall (2008b) gathered size data from taxonomic monographs for genera occurring in deep subtidal level-bottom assemblages from the Cambrian through the Devonian, and found an increase in mean genus size within several (but not all) taxa through this interval (Fig. 6), a trend explained by primarily by increased three-dimensionality (i.e., ‘fattening’ rather than increasing area). Kosnik et al. (2011) compiled data on the body sizes of 933 of the most commonly occurring brachiopod, gastropod, and bivalve genera in the Paleobiology Database (Fig.

7). This dataset is particularly relevant to energetic considerations because the included genera cumulatively account for a disproportionate percentage ($\geq 40\%$) of the recorded occurrences of these clades in each of 48 Phanerozoic time intervals (Kosnik et al., 2011). Where they overlap, the data sets of Kosnik et al. (2011) and Novack-Gottshall (2008b) show generally similar trends. Brachiopods increased in mean size by roughly an order of magnitude through the early to mid-Paleozoic, then exhibited relative stasis thereafter. The mean size of bivalves increased slightly in the Cambrian–Ordovician, and showed no secular trend thereafter, although there is some indication of a muted Late Triassic–Early Cretaceous maximum. Gastropods increased slightly in mean size through the Ordovician, declined slightly from the Silurian through the Triassic, and then increased slightly but rapidly in the mid-Jurassic, followed by relative stasis to the Recent. Chordates were not included in the Novack-Gottshall (2008b) or Kosnik et al. (2011) analyses, but Albert and Johnson (2012) recently examined the fossil record of fish, and found that their mean size increased substantially during the Cambrian–Silurian and then did not change substantially thereafter.

As with bioclastic content and bioturbation trends, there are relatively short-term decreases in mean body size associated with at least some of the major mass extinction events (see Hull and Darroch, 2013). The generality of this so-called ‘Lilliput effect’ (Urbanek, 1993) is disputed, but the pattern appears robust for some groups during or after the Permian–Triassic (Fraiser and Bottjer, 2004; Payne, 2005; He et al., 2007; Twitchett, 2007; Rego et al., 2012; but see Brayard et al., 2010) and Cretaceous–Paleogene (Aberhan et al., 2007) extinctions. The ecological-evolutionary meaning of the Lilliput Effect is controversial because there are several distinctly different ways in which such a pattern could arise (Harries and Knorr, 2009; Rego et al., 2012). The fact that many of the foraminiferan genera that survived the late Permian mass extinction experienced mean size reductions in the Early Triassic (Rego et al., 2012) suggests that the post-extinction interval was characterized by environmental conditions conducive to small size, but whether

FIGURE 6.—Cambrian–Devonian trends in the mean estimated body volume of genera occurring in deep subtidal soft-substrate fossil assemblages, reproduced with permission from Novack-Gottshall (2008b). →

FINNEGAN: QUANTIFICATION OF ENERGY TRENDS IN ANCIENT ECOSYSTEMS



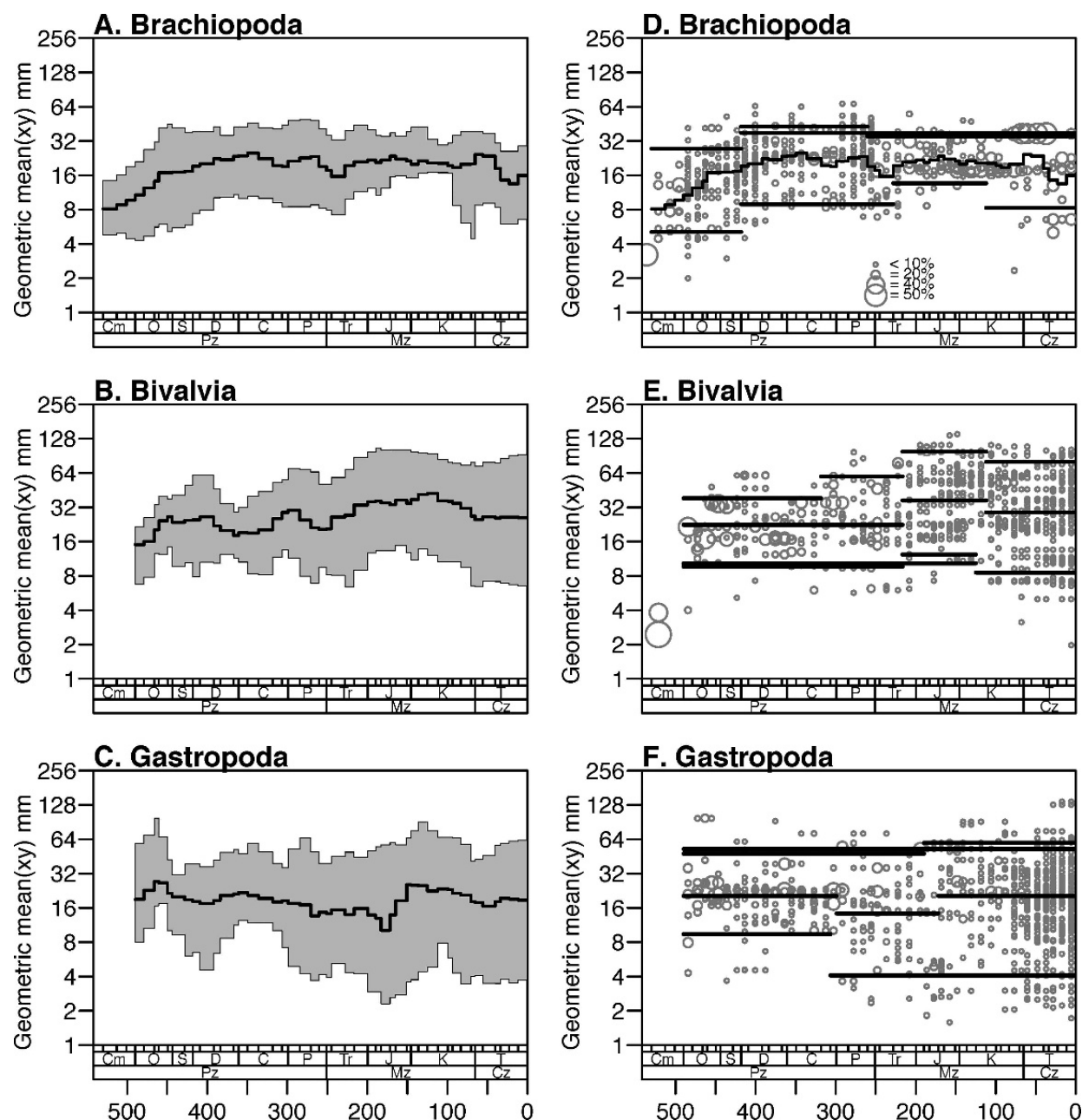


FIGURE 7.—Occurrence-weighted Phanerozoic trends in the shell sizes of the most common brachiopod, bivalve, and gastropod genera. Y axis shows geometric mean of length and width in millimeters on a \log_2 scale. In the left column (A–C), the solid black line is a three-point (three-bin) moving average of the mean occurrence-weighted shell size. Gray area is bounded by the 5th and 95th quantiles, which are used as proxies of the smallest and largest occurring shell sizes. In the right column (D–F) are the mean, 5th, and 95th quantiles (heavy black lines); each genus is plotted with a circle the size of which is proportional to its relative occurrence in the time bin. Reproduced with permission from Kosnik et al. (2011).

this was a consequence of low productivity, high temperature, low oxygen levels, low pH, or some combination of these factors is not yet known.

Skeletal size versus wet mass and ash-free dry mass

Paleontologists often use skeletal dimensions to estimate body volume; however, it is mass rather than volume (specifically, the total mass of

proteins, lipids, and carbohydrates; i.e., organic mass), that has the greatest influence on individual metabolic rate and energy content. Within a given group, there typically is a tight allometric relationship between skeletal dimensions and body mass, and the former can be treated as a direct proxy for the latter. It is often desirable to make biomass comparisons among different groups, however, and in this case there are other parameters that must be estimated.

For example, the Phanerozoic transition from generally brachiopod-dominated to bivalve-dominated paleocommunities is one of the most striking and studied paleoecological trends in the fossil record (Gould and Calloway, 1980; Thayer, 1983, 1986; Rhodes and Thompson, 1993; Clapham et al., 2006; Clapham and Bottjer, 2007), and one that has important implications for benthic energetic trends (Bambach, 1993). As has been pointed out by Peck (1992, 1993), rhychonelliform brachiopods are small animals occupying relatively voluminous shells, and the density of living tissue in rhychonelliform brachiopods commonly is an order of magnitude (or more) less than that of bivalves (Peck, 1992, 1993). To directly compare brachiopod and bivalve biomass therefore requires different models of the relationship between shell size and body mass for these two groups. Equations relating shell size to soft tissue mass have been determined for gastropods and bivalves by Powell and Stanton (1985) and for brachiopods and bivalves by Peck (1993).

Because fresh tissues contain large amounts of water, individuals are often weighed both before and after drying to determine wet mass (WM) and dry mass (DM). Dry mass includes a variable amount of mineral content, so organic mass is usually measured as ash-free dry mass (AFDM), which is DM minus the mass of the residuum left over following combustion in a muffle furnace or bomb calorimeter. This procedure also yields the energy content of the individual, usually given as J/mg AFDM.

Nearly 6000 energy content measurements, representing ~3500 species, have been compiled by Brey (2001). Mean ratios of ash-free dry mass to wet mass (AFDM/WM) and energy yield (J/mg AFDM) from this database are plotted for sixteen paleontologically important groups in Figure 8. Although there is little variation in mean J/mg AFDM across these taxa, there is considerable variation in AFDM/WM (Brey et al., 1988). It is notable that crinoids and articulate

(rhychonelliform) brachiopods, two of the taxa that commonly numerically dominate Paleozoic assemblages, have very low AFDM/WM ratios relative to Cenozoic dominants such as gastropods, bivalves, and decapods. In the case of crinoids, the reported AFDM/WM ratio may still be an overestimate for most Paleozoic taxa because data are primarily based on measurements of comatulids, which have high AFDM/WM relative to stalked crinoids (Baumiller and Labarbera, 1989). In the case of brachiopod versus bivalve, combining DM/cm³ estimates from Peck (1993) and AFDM/DM estimates from Brey (2001) suggests that bivalves typically have from 3 to 73 times the organic mass of brachiopods with equivalent skeletal volumes.

METABOLISM

Brey (2001) also compiled more than 20,000 measurements of resting metabolic rate (respiration) for aquatic invertebrates. Plotting metabolic rate against body mass (AFDM) illustrates that both body size and ambient temperature are strongly positively correlated with individual resting metabolic rate (energy * mass⁻¹ * time⁻¹) across phylogenetically, ecologically, and ontogenetically disparate individuals (Fig. 9). Whether size constrains individual metabolic rate or, as has been suggested, vice versa (Pauly, 2010), this observation is important for analyses of energetic trends in the fossil record because it suggests that, especially if temperature variation is reduced by controlling for depth and latitude (or by direct proxy measurements), body size measurements will capture most of the variation in individual metabolic rates within and between fossil assemblages (Powell and Stanton, 1985, 1996; Cummins et al., 1986; Finnegan and Droser, 2008; Finnegan et al., 2011).

The mass dependence of individual metabolic rate typically is expressed by an equation of the form:

$$B = B_0 M^b \quad (\text{Eq. 1})$$

where B = individual metabolic rate, M = body mass, B_0 is an empirically fit taxon-specific normalization constant, and b is a scaling coefficient that typically falls in the 2/3 to 1 range and commonly is very close to 3/4. The

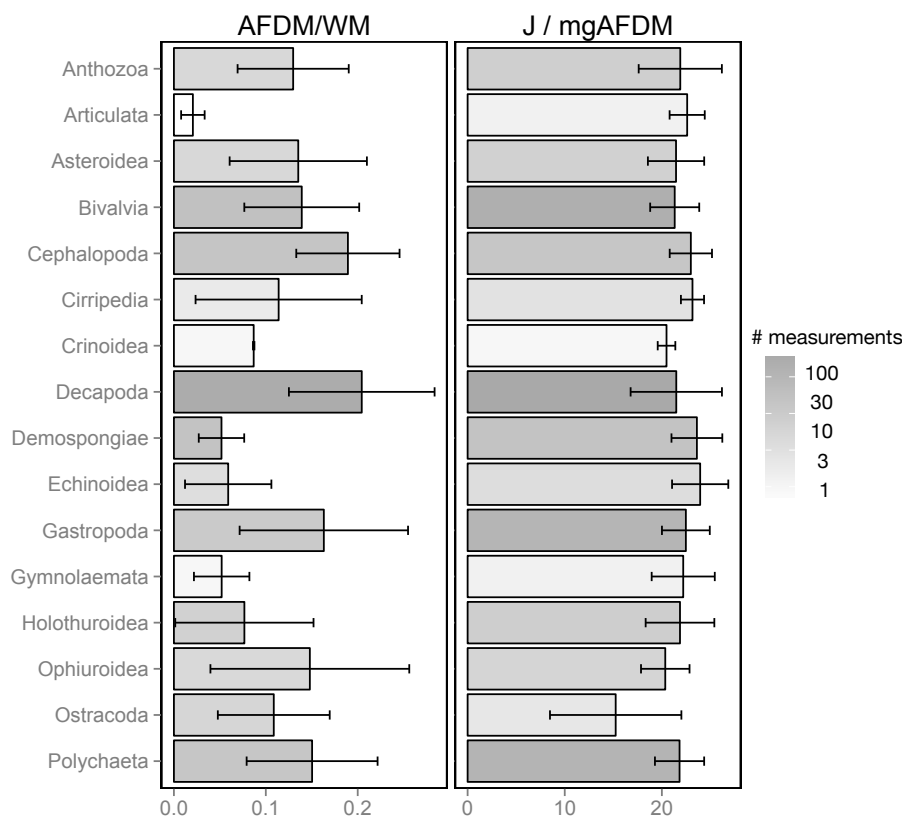


FIGURE 8.—Ash-free dry mass to wet mass ratios (AFDM/WM) and energy yields per unit ash-free dry mass (J/ mg AFDM) from Brey's (2001) database. Bars indicate means and error bars indicate 95% confidence intervals. Shading of bars indicates the number of measurements for each taxon.

temperature dependence of B in this formulation is traditionally expressed by inclusion of a Q_{10} term. For any value of $b < 1$, respiration rate per unit mass scales as a negative function of body mass (e.g., if b is $3/4$, respiration rate per unit mass scales as $m^{-1/4}$), so that large organisms require less energy per unit mass for respiration than do small organisms. The generality of $1/4$ power scaling in ecology and physiology and the potential mechanisms underlying these relationships have been the subject of intense debate over the past several years (e.g., West et al., 2003; Brown et al., 2004; Savage et al., 2004b, 2008; Glazier, 2005, 2010; Seibel and Drazen, 2007; White et al., 2007; Price et al., 2012). The metabolic theory of ecology (MTE; Gillooly et al., 2001; Allen et al., 2002; Savage et al., 2004a) posits that $3/4$ -power scaling of individual metabolic rate with body size is a universal feature of multicellular life that arise from the fractal nature of fluid distributary networks. The MTE reformulates Eq. 1 in explicitly thermodynamic terms to model the temperature-dependence of metabolic

biochemical reaction rates (West et al., 1997; Gillooly et al., 2001; Savage et al., 2004a):

$$B = B_0 e^{-E/kT} M^{3/4} \quad (\text{Eq. 2})$$

where T = temperature in $^{\circ}\text{K}$, B_0 is an empirically fit taxon-specific normalization constant, E is the average activation energy of rate-limiting biochemical reactions, and k is Boltzmann's constant. Although this model is highly controversial, it provides a useful framework for considering metabolic rates in the fossil record, and, for most paleoecological applications, very similar trends are obtained whether the MTE or a more traditional Q_{10} formulation is used. Most empirically determined Q_{10} formulations are close to 2, so that whether using the MTE or Q_{10} formulation, the effect of a 10°C increase in ambient temperature on individual metabolic rate is approximately equivalent to that of a $\sim 75\%$ increase in body mass (Fig. 10). The paleontological examples that are summarized below employ the MTE model and assume a b of

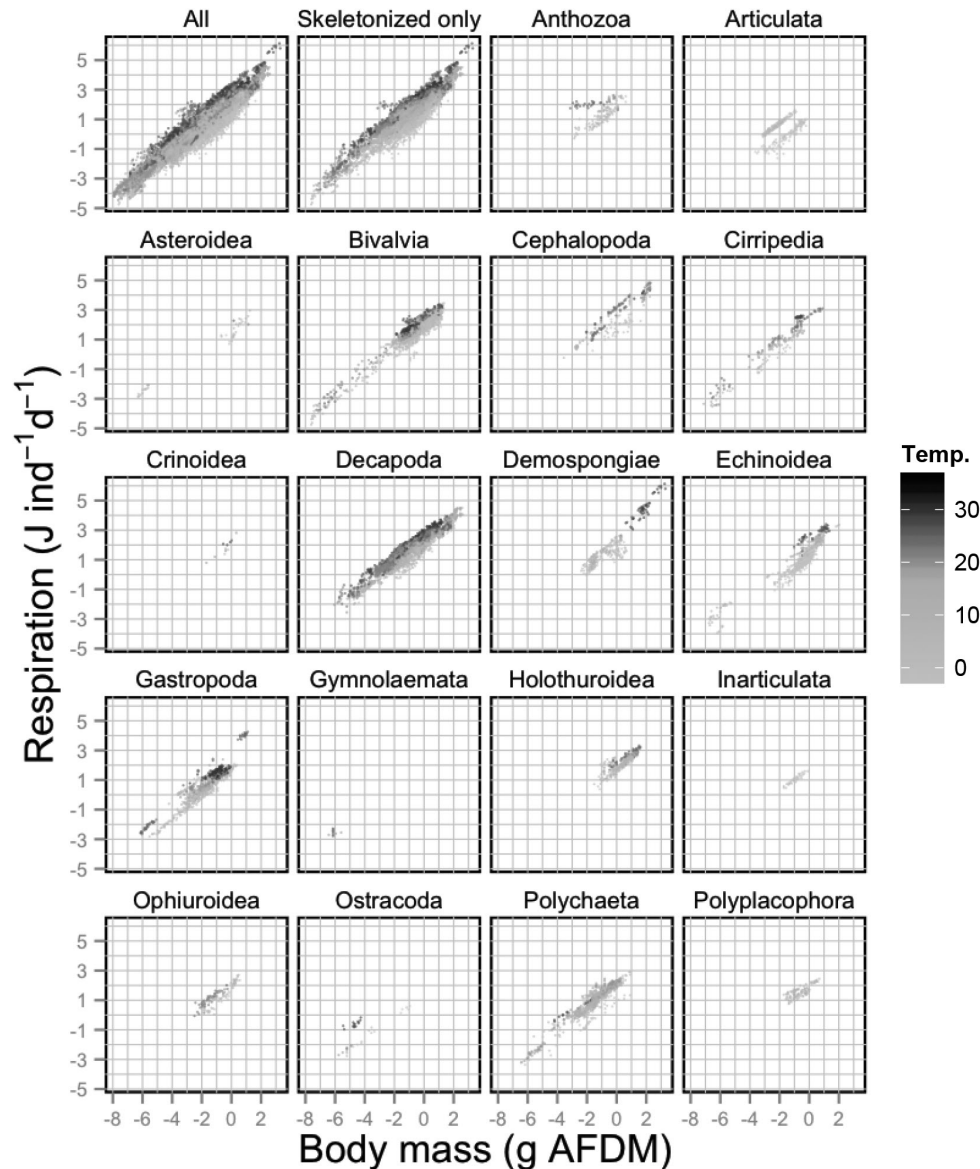


FIGURE 9.—Measurements of respiration plotted against body mass for all taxa (top left panel) and taxa that are at least partially skeletonized and/or paleontologically important (remaining panels). The temperature at which respiration was measured is indicated by the color scale. Although Brey (2001) reports body mass in energetic units (J), body masses are here plotted as g AFDM assuming a uniform conversion factor of 2.1×10^4 J / g AFDM (Fig. 7). The exceptionally large mass ranges exhibited by some taxa reflect inclusion of larval stages.

3/4, but this is not necessarily appropriate for all marine invertebrates under all conditions (Glazier, 2005, 2006; Seibel, 2007). Derivations of b and B_0 for various marine invertebrate groups can be found in numerous references, including Vladimirova (2001), Vladimirova et al. (2003), Glazier (2005), Seibel (2007), and Makarieva et al. (2008), or can be extracted from Brey's (2001) compilation.

As an alternative to linear models, Brey (2010) used a neural net model to model the

effects of body mass, temperature, depth, diet, and a host of other potential predictors on mass-specific metabolic rate. Predicted metabolic rates at a fixed body mass and temperature show considerable variation among the paleontologically important taxa included in Brey's (2001) database (Fig. 11), with echinoderms generally having the lowest predicted metabolic rates, and mollusks, particularly bivalves and cephalopods, having the highest predicted metabolic rates. This model

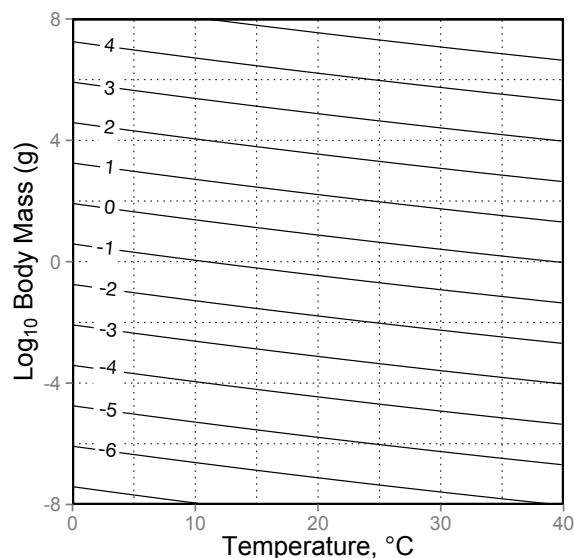


FIGURE 10.—The relative effects of temperature and body mass on the \log_{10} basal metabolic rate of a hypothetical individual according to the predictions of the metabolic theory of ecology (MTE). Mass range reflects the full range of marine metazoan body size (Bonner, 2006) and temperature range includes the biologically relevant range experienced by the vast majority of marine organisms. Contours indicate lines of constant \log_{10} basal metabolic rate (W). Q_{10} -based formulations for the mass- and temperature-dependence of basal metabolic rate give similar results.

estimates that the resting metabolic rate of a brachiopods is about half that of bivalves, a ratio that is comparable to previous estimates (but see Ballanti et al., 2012). Perhaps the most striking feature of these data is not the relative differences, but rather the narrow, approximately fourfold range of variation seen among phylogenetically and ecologically disparate clades. These results are consistent with other data suggesting that mass- and temperature-specific resting metabolic rates exhibit a very narrow range of variation across 20 orders of magnitude in body mass, implying conservation of fundamental metabolic biochemistry across all metazoa (Makarieva et al., 2008). The narrow range of mass- and temperature-specific resting metabolic rates means that, when estimating individual metabolic rates for fossil data, uncertainty regarding the conversion of skeletal size measurements to organic mass estimates (see above) often will be a much more important source of error than uncertainty about the mass-specific metabolic rates or the taxa in question.

A caveat is necessary concerning the use of basal metabolic rate as a proxy for metabolic

energy requirements. Basal metabolic rate measurements are made with the explicit goal of factoring out organismal behavior and activity level, but one of the most striking features of the benthic fossil record is a Phanerozoic increase in the proportion of at least facultatively motile species and individuals (Bush and Bambach, 2004, 2011; Bush et al., 2007). In addition, as has been emphasized by Bambach (1993, 1996), Vermeij (1987, 2004), Thayer (1983) and others, relative activity levels and power (*sensu* Vermeij, 2004) have likely increased even among motile taxa. Active metabolic rates are difficult to measure for benthic invertebrates and difficult to generalize to the ecosystem scale or integrate over organismal lifespans. Consequently, it is not easy to quantitatively estimate the energetic significance of Phanerozoic trends in motility and activity level. However, given that active and resting metabolic rates can differ quite substantially in some species (Seibel, 2007), and may scale differently with body size (Nagy, 2005), the effect may be large.

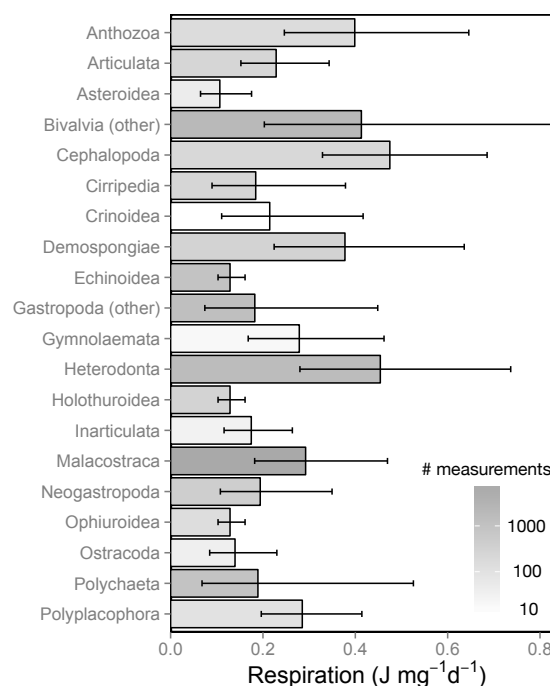


FIGURE 11.—Mass- and temperature-specific basal metabolic rate estimates (for an individual weighting 1 gram at an ambient temperature of 20° C) predicted by a neural net model formulated by Brey (2010). Bars indicate specific respiration rate and error bars indicate 95% confidence intervals. Shading of the bars indicates the number of measurements included in the training dataset.

ENERGETICS: INTEGRATING ABUNDANCE, BODY SIZE, AND METABOLISM

To date, the most thorough and complete approaches to analyzing the energetics of fossil assemblages have been outlined by Powell and Stanton (1985, 1996), Cummins et al. (1986), Staff et al. (1986), and Powell et al. (1992, 2001) in a series of papers on the living mollusk communities and subfossil skeletal assemblages of Copano Bay, Texas, and adjacent shelf settings. This model, which estimates the total amount of energy assimilated by each individual in a fossil assemblage over the course of its lifetime, has the form:

$$A = P_g + P_r + R \quad (\text{Eq. 3})$$

Where A is the total amount of energy assimilated by the individual over the course of its life, P_g is the proportion of lifetime net production allocated to somatic tissue growth, P_r is the proportion of lifetime net production allocated to reproduction, and R is the amount of energy respired over the individual's lifetime (Powell and Stanton, 1985, 1996). Powell and Stanton (1985) used this framework to estimate energy flow through four gastropod and one bivalve species preserved in the Eocene Stone City Formation, and showed that relative ecological importance as measured by energy flow differed substantially from ecological importance as measured by relative abundance.

The framework established by Powell and Stanton (1985) has several attractive properties. Because the individuals in a death assemblage have, by definition, completed their lives, it attempts to account for lifetime energy expenditures by integrating respiration, reproduction, and somatic growth costs from the age of larval settlement to the age of death. Large individuals in living assemblages have a disproportionate influence on energy fluxes because they account for a larger share of instantaneous respiration and biomass production, but this influence is magnified in the Powell and Stanton (1985) framework because large, dead individuals represent the integration of energy expenditures over a longer timespan than smaller dead individuals do.

The principal disadvantage of Powell and Stanton's (1985) approach for delineating trends

through time or across environments is that it requires: 1) determination of several parameters, including age at death of each individual and age of sexual maturity, that must be estimated either from knowledge of living relatives or from detailed investigation of life-history as recorded by the shells of each species (seasonal growth banding); and 2) completely size-censused fossil assemblages. The latter limitation is particularly problematic. The size-frequency distribution of individuals is the most important piece of information for estimating benthic energy fluxes (Powell and Stanton, 1985, 1996; Staff et al., 1985; Cummins et al., 1986), and is also an attractive paleoecological parameter because the distribution of energy flow through size classes appears to be a more temporally persistent attribute of paleocommunity structure than relative abundance structure (Powell and Stanton, 1996). Unfortunately, although there are many isolated case studies of within-assemblage size-frequency distributions in the paleontological literature, they tend to focus on single species or genera. Additional whole-assemblage studies are feasible in exceptionally well-preserved units, and would be a very useful contribution; meanwhile, a simpler approach may suffice to at least highlight broad trends.

Example I: Ordovician trilobites and brachiopods

Finnegan and Droser (2008) integrated genus-level body size estimates with relative abundance data from shallow to deep subtidal Laurentian fossil assemblages to examine Ordovician trends in the biomass and metabolic demands of trilobites and brachiopods, the dominant components of Sepkoski's (1981) Cambrian and Paleozoic Evolutionary Faunas (EF). Their analysis assumed that: 1) the maximum body size recorded for a genus in a given interval is a reasonable proxy for the mean size of individuals in that genus; 2) the total density of individuals on the seafloor was constant or increasing through the Ordovician (a conservative assumption given the biomass and bioturbation trends discussed above); and 3) fossil size-frequency distributions are, if not comparable to those of the original living assemblages (a problematic assumption, as previously discussed), subject to relatively consistent preservational biases.

Unlike Powell and Stanton's (1985) analytical framework, Finnegan and Droser's (2008) approach does not quantify integrated lifetime

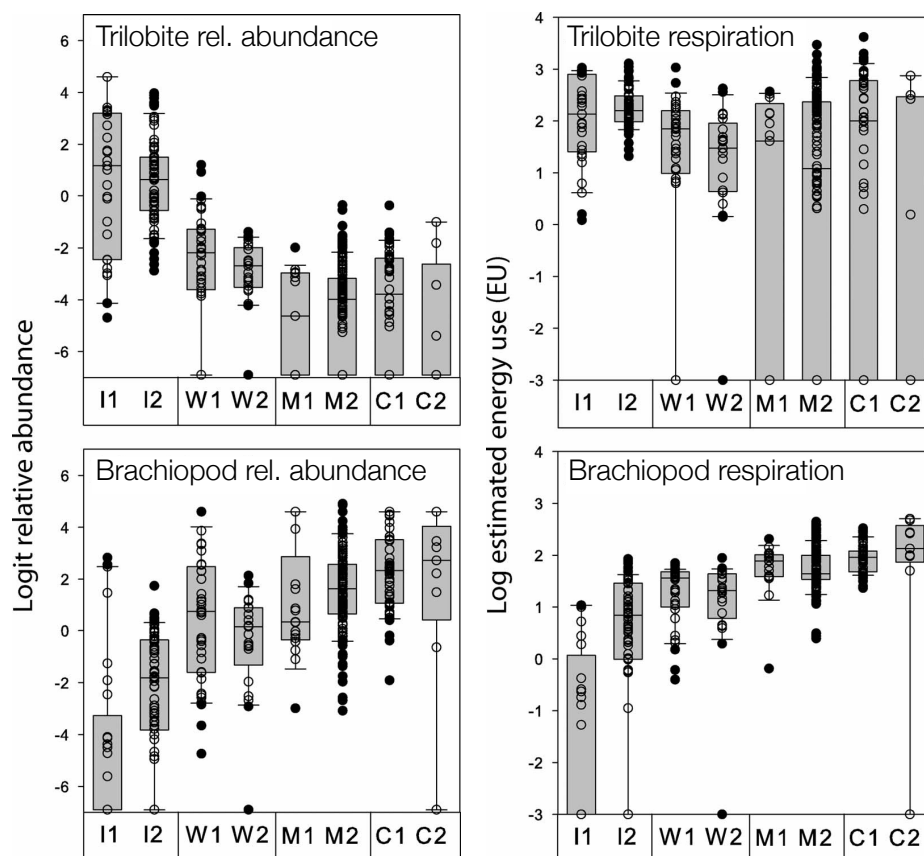


FIGURE 12.—Ordovician trends in the relative abundance (left panels) and in the estimated aggregate metabolic energy requirements (right panels) of trilobites (top panels) and brachiopods (bottom panels) from shallow to deep subtidal Laurentian paleocommunities. Whereas the relative abundance of trilobites declines considerably throughout the Ordovician, their estimated metabolic energy requirements remain relatively stable, a trend largely driven by the presence of the exceptionally large asaphid genus *Isotelus* in many Late Ordovician paleocommunities. I1: 489.0–476.5 Ma, I2: 476.5–472 Ma, W1: 472–470 Ma, W2: 470–460.5 Ma, M1: 460.5–454.5 Ma, M2: 454.5–451 Ma, C1: 451–448.5 Ma, C2: 448.5–444 Ma. Modified from Finnegan and Droser (2005).

energy expenditures. Rather, it focuses on estimating the instantaneous energy flux that would have been required to maintain the individual metabolic rates of all individuals in the assemblage had they been alive simultaneously. This is based on a simple extension of Eq. 2 in which per-genus metabolic rate estimates are weighted by their relative (or, if available, absolute) abundances:

$$B_{agg} = \sum_{i=1}^N A_i B_{0i} e^{-E_i/kT} M_i^{3/4} \quad (\text{Eq. 4})$$

where B_{agg} is the aggregate energy required for respiration, N is the total number of genera in the assemblage, B_{0i} is a taxon specific normalization constant, and M_i and A_i are the mean body mass

and the abundance of the i th genus. Respiration typically accounts for 30–80% of lifetime energy expenditures in marine invertebrates (Huebner and Edwards, 1981; Barkai and Griffiths, 1988; Morton and Chan, 1999) and although this approach does not explicitly estimate biomass production rates, there is a moderately strong positive correlation between mean annual respiration and production rates in animal populations, including marine invertebrates (Humphreys, 1979; Schwinghamer et al., 1986).

Applying Eq. 4 to genera in Ordovician fossil assemblages reveals that, although the average relative abundance of trilobites declined substantially over this interval as that of brachiopods increased, their average metabolic demand remained roughly constant (Fig. 12), a pattern driven primarily by occurrences of the widespread and exceptionally large asaphid genus

Isotelus. In this case, focusing on biomass and energetics rather than richness and abundance clarifies that the apparent displacement of trilobites from an onshore setting by the radiating Paleozoic fauna (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985) was likely attributable to passive numerical dilution rather than competitive interaction (Westrop et al., 1995).

Example II: Meso–Cenozoic gastropods

Finnegan et al. (2011) extended this approach to evaluate the biomass and energetic requirements of gastropod assemblages from before and after the Marine Mesozoic Revolution (Vermeij, 1977, 1987; Aberhan et al., 2006). To ameliorate the limitations imposed by lack of sufficient numbers of size-censused fossil assemblages, Finnegan et al. (2011) used size-frequency distributions of living gastropod populations to parameterize a model relating the maximum size of a species to its mean size. This model was able to accurately predict the mean individual sizes of nine fossil species from a size-censused Middle Triassic assemblage. Using modeled mean-size estimates to generate species-specific log-normal size distributions, and assigning individual sizes by a random draw from these distributions, Finnegan et al. (2011) broadly reproduced the modes and shapes of size-censused gastropod assemblages. This is a promising approximation when individual size data are lacking, but requires further parameterization and testing. Finnegan et al. (2011) modeled 432 fossil and 38 living or subfossil tropical to subtropical gastropod assemblages using this approach, and found that average individual metabolic rate increased from a Lower Triassic low (Fraiser and Bottjer, 2004; Payne, 2005) to a Middle and Late Triassic plateau, increased by ~150% between the Late Triassic and the Early Cretaceous (Fig. 13), then remained relatively constant thereafter despite continued global diversification of gastropods. This increase was driven primarily by a substantial increase in both mean and maximum body size. The degree to which this reflects greater longevity versus faster growth rates is not known, but could be investigated by using stable isotope sclerochronology to compare well-preserved aragonitic individuals, such as those from the Middle Triassic St. Cassian Formation (Zardini, 1978; Nützel et al., 2010), with more recent shells.

As has been noted by Bambach (1993, 1996),

Vermeij (1977, 1987, 2002, 2004), and others, the explosive Meso–Cenozoic diversification of the Neogastropoda is particularly notable for its energetic implications. Whereas most Paleozoic and early Mesozoic gastropods are thought to have been detritivores and filter feeders, most modern marine gastropods are carnivores. The neogastropod diversification is a major component of the Phanerozoic increase in the proportion of predators in shelly fossil assemblages (Bambach, 1985; Bambach et al., 2002; Bambach and White, 2002), and implies either a commensurate increase in primary production and prey biomass, or competitive displacement of other nonskeletonized carnivorous groups. Assuming a typical trophic transfer efficiency of ~10% and minimal gastropod-on-gastropod predation, Finnegan et al. (2011) estimated that the net primary production required to support respiration of an average gastropod individual rose as much as eightfold during the Mesozoic. Trends in primary productivity are difficult to estimate from fossil and geochemical records, but the diversification trajectory of red group phytoplankton (Falkowski et al., 2004; Katz et al., 2004; van de Schootbrugge et al., 2005; van de Schootbrugge and Gollner, 2013) roughly coincides with the observed increase in gastropod size.

SUMMARY: CHALLENGES AND PROSPECTS

This review has covered only a handful of the many papers that pertain in one way or another to understanding the long-term patterns highlighted by Bambach (1993) two decades ago. Even with a narrow focus on the benthic marine record of skeletonized groups, the scope of the subject is so broad that entire fields of study, such as paleoceanography, micropaleontology, and geochemistry that have much to say on this topic have been omitted. I have also tried to avoid restating the qualitative arguments regarding secular energetic trends already laid out by Bambach (1993) and others. These arguments are as compelling today as they were twenty years ago, and the major advance in the interim has been the exponential growth of relevant data.

Quantification of energetic trends in the fossil record remains a very difficult problem that involves aggregating disparate types of data that are often fragmentary and poorly defined. Nearly all types of fossil data that are discussed here are

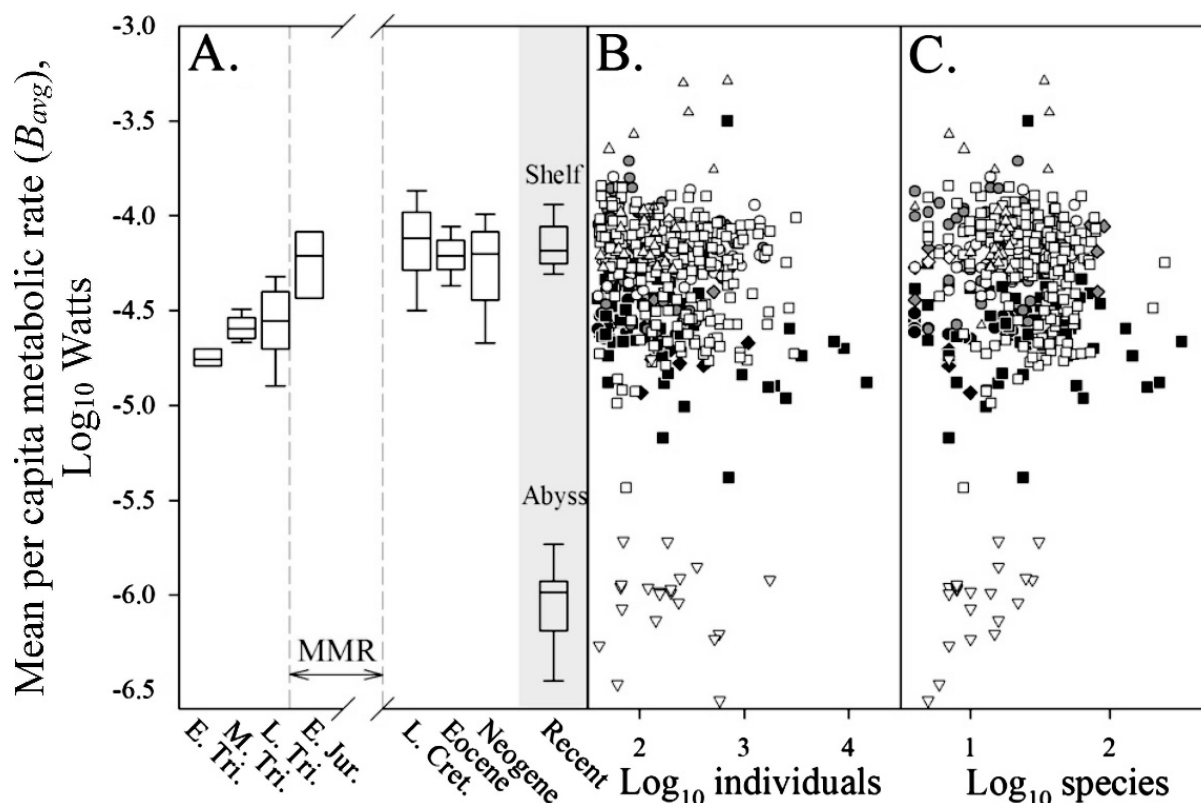


FIGURE 13.—A) Boxplots showing the distribution of \log_{10} mean individual metabolic rate (B_{avg}) estimates for Triassic, Early Jurassic, and Late Cretaceous–Neogene fossil gastropod assemblages, modern shallow subtidal tropical assemblages from St. Croix (Miller, 1988), and modern slope-abyssal assemblages from the northwest Atlantic (McClain, 2004). Horizontal bars represent median values, boxes enclose the 25th through 75th percentiles, and whiskers indicate the 2.5th and 97.5th percentiles. Double-ended arrow labeled MMR indicates the interval over which the Mesozoic Marine Revolution occurred; break indicates a sampling gap of 75 Myr between the Early Jurassic and the Late Cretaceous. B), C) B_{avg} plotted against: B) the total number of individuals; and C) species in each assemblage. Black circles = Early Triassic; black diamonds = Middle Triassic; black squares = Late Triassic; gray circles = Early Jurassic; gray diamonds = Late Cretaceous; white circles = Eocene; white diamonds = Neogene; white triangles = Recent St. Croix; white inverted triangles = Recent slope-abyssal. Reproduced with permission from Finnegan et al. (2011).

characterized by extreme variability in time and space. This variability has many sources. Some of it is attributable to taphonomic information loss, which is a critical concern because paleoenergetic estimates depend so heavily on interpretation of fossil abundance and body size distributions. Taphonomic processes and their effect on the preservation of diversity and abundance gradients have been extensively studied (Tomašových and Kidwell, 2009), but no specifically energetic comparison of living communities and their co-occurring death assemblages has been published to date. Such a comparison is feasible with the Copano Bay dataset compiled by Staff, Cummins, Powell and colleagues, but there are few other datasets that include abundance and individual body size for both live and dead individuals—a

live-dead energetic comparison encompassing a broader range of environments would be challenging, but would help to answer critical questions about the fidelity with which primary spatial and environmental energetic gradients are preserved in the fossil record. It is likely that much of the abundance and body-size variation in fossil assemblages is not caused by taphonomic distortion but by genuine gradients that played as important a role in controlling the distribution of habitat, nutrients, and energy in ancient oceans as they do in modern oceans. For example, although the Triassic–Recent increase in the mean size and respiration rate of gastropods in shallow subtropical settings is notable, there is considerable overlap in this metric between Triassic and post-Jurassic assemblages, and the

differences between them are dwarfed by the differences between modern shelf and abyssal faunas (Figs. 1, 13). Known environmental gradients need to be controlled for in order to increase the likelihood of discerning temporal signals above normal environmental noise. Despite the low signal/noise ratio, some features of this record have emerged as clear and robust: increases in bioturbation intensity, bioclastic production, and mean body size associated with the Ordovician Biodiversification are one example, as are the mirror-image trends associated with the Permo–Triassic extinction and recovery interval. Other features of the fossil record, such as the diffuse and protracted but cumulatively large changes in marine ecosystems associated with the Marine Mesozoic Revolution, are still comparatively enigmatic and poorly defined (Aberhan et al., 2006).

Numerous drivers that have been suggested as explanations for some of these trends have not been discussed, and include, but are not limited to, climate change (via its numerous potential effects on primary productivity, the efficiency of export of net primary production to benthic ecosystems, body size, and respiration efficiency), progressive oxygenation of the oceans (Dahl et al., 2010), enhanced nutrient supply from volcanism (Vermeij, 1995) or from the expansion and diversification of terrestrial ecosystems (Bambach, 1993, 1999; Algeo and Scheckler, 1998), and increased nutrient recycling due to increased bioturbation (Thayer, 1983). This is dictated in part by space constraints but also by the wish to focus narrowly on issues of quantification. Although available data can test some of these hypotheses (e.g., the Jurassic increase in gastropod body size and biomass noted by Finnegan et al. (2011) and Kosnik et al. (2011) is too early to have been driven by increased nutrient flux from Cretaceous expansion of terrestrial angiosperms (Bambach, 1993, 1999)), testing them more rigorously will require more and better resolved paleobiological and environmental proxy data, and more sophisticated models than are currently available. The development and increasingly widespread application of stable isotopic and organic proxies continues to improve our understanding of the physical, chemical, and microbiological history of marine habitats, and new paleontological approaches such as sclerochronology, offer increased insights into the physiologies, ecologies, and life-histories of extinct species.

Combined with the various field and analytical approaches summarized here, these emerging approaches have great potential to illuminate the ways in which Earth systems processes have shaped the ecology and evolution of the marine biota over time, and promise to make the next twenty years as exciting and productive as the last twenty years have been.

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REFERENCES

- ABERHAN, M., W. KIESSLING, AND F. T. FÜRSICH. 2006. Testing the role of biological interactions in the evolution of mid-Mesozoic marine benthic ecosystems. *Paleobiology*, 32:259–277.
- ABERHAN, M., S. WEIDEMEYER, W. KIESSLING, R. A. SCASSO, AND F. A. MEDINA. 2007. Faunal evidence for reduced productivity and uncoordinated recovery in Southern Hemisphere Cretaceous–Paleogene boundary sections. *Geology*, 35:227–230.
- ADRAIN, J. M., S. R. WESTROP, B. D. E. CHATTERTON, AND L. RAMSKOLD. 2000. Silurian trilobite alpha diversity and the end-Ordovician mass extinction. *Paleobiology*, 26:625–646.
- AITCHISON, J. 1982. The statistical analysis of compositional data (with discussion). *Journal of the Royal Statistical Society Series B (Statistical Methodology)*, 44:139–177.
- ALBERT, J. A., AND D. M. JOHNSON. 2012. Diversity and evolution of body size in fishes. *Evolutionary Biology*, 39:324–340.
- ALGEO, T. J., AND S. E. SCHECKLER. 1998. Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 353:113–128.
- ALLEN, A. P., J. H. BROWN, AND J. F. GILLOOLY. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297:1545–1548.
- ALROY, J., M. ABERHAN, D. J. BOTTJER, M. FOOTE, F. T. FÜRSICH, P. J. HARRIES, A. J. W. HENDY, S. M.

- HOLLAND, L. C. IVANY, AND W. KIESSLING. 2008. Phanerozoic trends in the global diversity of marine invertebrates. *Science*, 321:97–100.
- BALLANTI, L. A., A. TULLIS, AND P. D. WARD. 2012. Comparison of oxygen consumption by *Terebratalia transversa* (Brachiopoda) and two species of pteriomorph bivalve molluscs: implications for surviving mass extinctions. *Paleobiology*, 38:525–537.
- BAMBACH, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology*, 3:152–167.
- BAMBACH, R. K. 1985. Classes and adaptive variety; the ecology of diversification in marine faunas through the Phanerozoic, p. 191–253. *In* J. W. Valentine (ed.), *Phanerozoic Diversity Patterns: Profiles in Macroevolution*. Princeton University Press, Princeton, New Jersey.
- BAMBACH, R. K. 1993. Seafood through time—changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology*, 19:372–397.
- BAMBACH, R. K. 1999. Energetics in the global marine fauna: A connection between terrestrial diversification and change in the marine biosphere. *Geobios*, 32:131–144.
- BAMBACH, R. K., A. H. KNOLL, AND J. J. SEPKOSKI. 2002. Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. *Proceedings of the National Academy of Sciences of the United States of America*, 99:6854–6859.
- BAMBACH, R. K., AND R. D. WHITE. 2002. Supporting predators: changes in the global ecosystem inferred from changes in predator diversity, p. 319–352. *In* M. Kowalewski and P. H. Kelley (eds.), *The Fossil Record of Predation*. The Paleontological Society Papers 8, Yale Press, New Haven.
- BARKAI, R., AND C. GRIFFITHS. 1988. An energy budget for the South African abalone *Haliotis midae* Linnaeus. *Journal of Molluscan Studies*, 54:43–51.
- BAUMILLER, T. K., AND M. LABARBERA. 1989. Metabolic rates of Caribbean crinoids (Echinodermata), with special reference to deep-water stalked and stalkless taxa. *Comparative Biochemistry and Physiology Part A: Physiology*, 93:391–394.
- BELANGER, C. L., D. JABLONSKI, K. ROY, S. K. BERKE, A. Z. KRUG, AND J. W. VALENTINE. 2012. Global environmental predictors of benthic marine biogeographic structure. *Proceedings of the National Academy of Sciences*, 109:14046–14051.
- BERKE, S. K., D. JABLONSKI, A. Z. KRUG, K. ROY, AND A. TOMAŠOVÝCH. 2013. Beyond Bergmann's rule: size-latitude relationships in marine Bivalvia worldwide. *Global Ecology and Biogeography*, 22:173–183.
- BONNER, J. T. 2006. *Why Size Matters: From Bacteria to Blue Whales*. Princeton University Press, Princeton, New Jersey.
- BOTTIER, D. J., J. W. HAGADORN, AND S. Q. DORNBOS. 2000. The Cambrian substrate revolution. *GSA Today*, 10:1–7.
- BRANDT, D. S. 1986. Preservation of event beds through time. *PALAIOS*, 1:92–96.
- BRAYARD, A., A. NÜTZEL, D. A. STEPHEN, K. G. BYLUND, J. JENKS, AND H. BUCHER. 2010. Gastropod evidence against the Early Triassic Lilliput effect. *Geology*, 38:147–150.
- BREY, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. v01.2. Alfred Wegener Institute for Polar and Marine Research, Germany. <http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html>.
- BREY, T. 2010. An empirical model for estimating aquatic invertebrate respiration. *Methods in Ecology and Evolution*, 1:92–101.
- BREY, T., H. RUMOHR, AND S. ANKAR. 1988. Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *Journal of Experimental Marine Biology and Ecology*, 117:271–278.
- BROCKS, J. J., AND A. PEARSON. 2005. Building the biomarker Tree of Life. *Reviews in Mineralogy and Geochemistry*, 59:233–258.
- BROWN, E. L., B. J. E. CHARNOV, G. B. WEST, AND H. JAMES. 1999. Allometric scaling of production and life-history variation in vascular plants. *Nature*, 401:866–907.
- BROWN, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- BROWN, J. H., J. F. GILLOOLY, A. P. ALLEN, V. M. SAVAGE, AND G. B. WEST. 2004. Toward a metabolic theory of ecology. *Ecology*, 85:1771–1789.
- BROWN, J. H., AND B. A. MAURER. 1989. Macroecology: the division of food and space among species on continents. *Science*, 243:1145–1150.
- BUSH, A. M., AND R. K. BAMBACH. 2004. Are secular changes in tiering, motility, and predation real? Quantifying and testing changes in ecospace use between the Paleozoic and Cenozoic. *Geological Society of America Annual Meeting Abstracts with Program*, 36:457.
- BUSH, A. M., AND R. K. BAMBACH. 2011. Paleoeccologic megatrends in marine metazoa. *Annual Review of Earth and Planetary Science*, 39:241–269.
- BUSH, A. M., R. K. BAMBACH, AND G. M. DALEY. 2007. Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology*, 33:76–97.
- BUSH, A. M., R. K. BAMBACH, AND J. T. PARRISH.

2004. Did alpha diversity increase during the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases. *Journal of Geology*, 112:625–642.
- BUTTERFIELD, N. J. 2011. Was the Devonian radiation of large predatory fish a consequence of rising atmospheric oxygen concentration? *Proceedings of the National Academy of Sciences*, 108:E28.
- CLAPHAM, M. E., AND D. J. BOTTJER. 2007. Permian marine paleoecology and its implications for large-scale decoupling of brachiopod and bivalve abundance and diversity during the Lopingian (Late Permian). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 249:283–301.
- CLAPHAM, M. E., D. J. BOTTJER, C. M. POWERS, N. BONUSO, M. L. FRAISER, P. J. MARENCO, S. Q. DORNBOS, AND S. B. PRUSS. 2006. Assessing the ecological dominance of Phanerozoic marine invertebrates. *PALAIOS*, 21:431–441.
- CLOUD, P. 1972. A working model of the primitive Earth. *American Journal of Science*, 272:537–548.
- CUMMINS, H., E. POWELL, R. STANTON, JR., AND G. STAFF. 1986. The size-frequency distribution in palaeoecology: effects of taphonomic processes during formation of molluscan death assemblages in Texas bays. *Palaeontology*, 29:495–518.
- DAHL, T. W., E. U. HAMMARLUND, A. D. ANBAR, D. P. G. BOND, B. C. GILL, G. W. GORDON, A. H. KNOLL, A. T. NIELSEN, N. H. SCHOVSBO, AND D. E. CANFIELD. 2010. Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *Proceedings of the National Academy of Sciences*, 107:17911–17915.
- DAMUTH, J. 1991. Of size and abundance. *Nature*, 351:268–269.
- DAVIES, D. J., E. N. POWELL, AND R. J. STANTON. 1989. Relative rates of shell dissolution and net sediment accumulation—a commentary: can shell beds form by the gradual accumulation of biogenic debris on the sea floor? *Lethaia*, 22:207–212.
- DE LEO, F. C., C. R. SMITH, A. A. ROWDEN, D. A. BOWDEN, AND M. R. CLARK. 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 277:2783–2792.
- DINMORE, T. A., AND S. JENNINGS. 2004. Predicting abundance-body mass relationships in benthic infaunal communities. *Marine Ecology-Progress Series*, 276:289–292.
- DROSER, M. L., AND D. J. BOTTJER. 1988. Trends in depth and extent of bioturbation in Cambrian carbonate marine environments, western United States. *Geology*, 16:233–236.
- DROSER, M. L., AND D. J. BOTTJER. 1989. Ordovician Increase in extent and depth of bioturbation—implications for understanding early Paleozoic ecospace utilization. *Geology*, 17:850–852.
- DROSER, M., AND D. BOTTJER. 1993. Trends and patterns of Phanerozoic ichnofabrics. *Annual Review of Earth and Planetary Sciences*, 21:205–225.
- ENQUIST, B. J., E. P. ECONOMO, T. E. HUXMAN, A. P. ALLEN, D. D. IGNACE, AND J. F. GILLOOLY. 2003. Scaling metabolism from organisms to ecosystems. *Nature*, 423:639–642.
- ERNEST, S. K. M., B. J. ENQUIST, J. H. BROWN, E. L. CHARNOV, J. F. GILLOOLY, V. M. SAVAGE, E. P. WHITE, F. A. SMITH, E. A. HADLY, J. P. HASKELL, S. K. LYONS, B. A. MAURER, K. J. NIKLAS, AND B. TIFFNEY. 2003. Thermodynamic and metabolic effects on the scaling of production and population energy use. *Ecology Letters*, 6:990–995.
- FALKOWSKI, P. G., M. E. KATZ, A. H. KNOLL, A. QUIGG, J. A. RAVEN, O. SCHOFIELD, AND F. J. R. TAYLOR. 2004. The evolution of modern eukaryotic phytoplankton. *Science*, 305:354–360.
- FINNEGAN, S., AND M. L. DROSER. 2005. Relative and absolute abundance of trilobites and rhyconelliform brachiopods across the Lower/Middle Ordovician boundary, eastern Basin and Range. *Paleobiology*, 31:480–502.
- FINNEGAN, S., AND M. L. DROSER. 2008. Body size, energetics, and the Ordovician restructuring of marine ecosystems. *Paleobiology*, 34:342–359.
- FINNEGAN, S., N. A. HEIM, S. E. PETERS, AND W. W. FISCHER. 2012. Climate change and the selective signature of the Late Ordovician mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, 109:6829–34.
- FINNEGAN, S., C. M. MCCLAIN, M. A. KOSNIK, AND J. L. PAYNE. 2011. Escargots through time: an energetic comparison of marine gastropod assemblages before and after the Mesozoic Marine Revolution. *Paleobiology*, 37:252–269.
- FRAISER, M. L., AND D. J. BOTTJER. 2004. The non-actualistic Early Triassic gastropod fauna: A case study of the Lower Triassic Sinbad Limestone member. *PALAIOS*, 19:259–275.
- GILLOOLY, J. F., J. H. BROWN, G. B. WEST, V. M. SAVAGE, AND E. L. CHARNOV. 2001. Effects of size and temperature on metabolic rate. *Science*, 293:2248–2251.
- GLAZIER, D. S. 2005. Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews of the Cambridge Philosophical Society*, 80:611–62.
- GLAZIER, D. S. 2006. The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *Bioscience*, 56:325–332.
- GLAZIER, D. S. 2010. A unifying explanation for diverse metabolic scaling in animals and plants. *Biological Reviews of the Cambridge Philosophical Society*, 85:111–38.
- GOULD, S. J. AND CALLOWAY, C. B. 1980. Clams and

- brachiopods—ships that pass in the night. *Paleobiology*, 6:383–396.
- GRAYSON, D. K. 1984. Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas. Studies in Archaeological Science, Academic Press, London.
- HARRIES, P. J., AND P. O. KNORR. 2009. What does the ‘Lilliput Effect’ mean? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 284:4–10.
- HE, W., G. R. SHI, Q. FENG, M. J. CAMPI, S. GU, J. BU, Y. PENG, AND Y. MENG. 2007. Brachiopod miniaturization and its possible causes during the Permian–Triassic crisis in deep water environments, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 252:145–163.
- HEIM, N. A., AND S. E. PETERS. 2010. Covariation in macrostratigraphic and macroevolutionary patterns in the marine record of North America. *Geological Society of America Bulletin* 123:620–630.
- HUEBNER, J., AND D. EDWARDS. 1981. Energy budget of the predatory marine gastropod *Polinices duplicatus*. *Marine Biology*, 61:221–226.
- HULL, P. M., AND S. A. F. DARROCH. 2013. Mass extinctions and the structure and function of ecosystems, p. 115–156. *In* A. M. Bush, S. B. Pruss, and J. L. Payne (eds.), *Ecosystem Paleobiology and Geobiology*, The Paleontological Society Papers 19. Yale Press, New Haven.
- HULL, P. M., R. D. NORRIS, T. J. BRALOWER, AND J. D. SCHUETH. 2011. A role for chance in marine recovery from the end-Cretaceous extinction. *Nature Geoscience*, 4:856–860.
- HUMPHREYS, W. F. 1979. Production and respiration in animal populations. *Journal of Animal Ecology*, 48:427–453.
- HUNT, G., AND K. ROY. 2006. Climate change, body size evolution, and Cope's Rule in deep-sea ostracodes. *Proceedings of the National Academy of Sciences of the United States of America*, 103:1347–1352.
- IVANY, L. C., AND B. T. HUBER (EDS). 2012. Reconstructing Earth's Deep-Time Climate—The State of the Art in 2012. The Paleontological Society Papers 18, Yale Press, New Haven.
- JENNINGS, S., J. K. PINNEGAR, N. V. POLUNIN, AND T. W. BOON. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70:934–944.
- JOHNSON, N. A., J. W. CAMPBELL, T. S. MOORE, M. A. REX, R. J. ETTER, C. R. MCCLAIN, AND M. D. DOWELL. 2007. The relationship between the standing stock of deep-sea macrobenthos and surface production in the western North Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers*, 54:1350–1360.
- KAARIAINEN, J. I., AND B. J. BETT. 2006. Evidence for benthic body size miniaturization in the deep sea. *Journal of the Marine Biological Association of the United Kingdom*, 86:1339–1345.
- KATZ, M. E., B. S. CRAMER, A. FRANZESE, B. R. HÖNISCH, K. G. MILLER, Y. ROSENTHAL, AND J. D. WRIGHT. 2010. Traditional and emerging geochemical proxies in Foraminifera. *The Journal of Foraminiferal Research*, 40:165–192.
- KATZ, M. E., Z. V. FINKEL, D. GRZEBYK, A. H. KNOLL, AND P. G. FALKOWSKI. 2004. Evolutionary trajectories and biogeochemical impacts of marine eukaryotic phytoplankton. *Annual Review of Ecology Evolution and Systematics*, 35:523–556.
- KERR, S. R., L. M. DICKIE, AND L. M. KERR AND S. R. DICKIE. 2001. *The Biomass Spectrum: A Predator-Prey Theory of Aquatic Production*. Columbia University Press, New York.
- KIDWELL, S. M. 1986. Models for fossil concentrations: paleobiologic implications. *Paleobiology*, 12:6–24.
- KIDWELL, S. M., AND P. J. BRECHLEY. 1994. Patterns in bioclastic accumulation through the Phanerozoic; changes in input or in destruction? *Geology*, 22:1139–1143.
- KIDWELL, S. M., AND P. J. BRECHLEY. 1996. Evolution of the fossil record: Thickness trends in marine skeletal accumulations and their implications, p. 290–336. *In* D. H. Erwin, D. Jablonski, and J. H. Lipps (eds.), *Evolutionary Paleobiology*. University of Chicago Press, Chicago.
- KIDWELL, S. M., F. T. FUERSICH, T. AIGNER, AND R. D. K. THOMAS. 1986. Conceptual framework for the analysis and classification of fossil concentrations. *PALAIOS*, 1:228–238.
- KIRCHMAN, D. L., X. A. G. MORÁN, AND H. DUCKLOW. 2009. Microbial growth in the polar oceans—role of temperature and potential impact of climate change. *Nature Reviews Microbiology*, 7:451–459.
- KIRCHNER, J. W., AND A. WEIL. 2000. Delayed biological recovery from extinctions throughout the fossil record. *Nature*, 404:177–180.
- KOSNIK, M. A. 2005. Changes in Late Cretaceous–early Tertiary benthic marine assemblages: analyses from the North American coastal plain shallow shelf. *Paleobiology*, 31:459–479.
- KOSNIK, M. A., J. ALROY, A. K. BEHRENSMEYER, F. T. FÜRSICH, R. A. GASTALDO, S. M. KIDWELL, M. KOWALEWSKI, R. E. PLOTNICK, R. R. ROGERS, AND P. J. WAGNER. 2011. Changes in shell durability of common marine taxa through the Phanerozoic: evidence for biological rather than taphonomic drivers. *Paleobiology*, 37:303–331.
- KOSNIK, M. A., D. JABLONSKI, R. LOCKWOOD, AND P. M. NOVACK-GOTTSHALL. 2006. Quantifying molluscan body size in evolutionary and ecological analyses: Maximizing the return on data-collection efforts. *PALAIOS*, 21:588–597.

- KOWALEWSKI, M., A. DULAI, AND F. T. FÜRSICH. 1998. A fossil record full of holes: The Phanerozoic history of drilling predation. *Geology*, 26:1091–1094.
- LAWS, E. A., P. G. FALKOWSKI, W. O. SMITH, H. DUCKLOW, AND J. J. MCCARTHY. 2000. Temperature effects on export production in the open ocean. *Global Biogeochemical Cycles*, 14:1231–1246.
- LI, X., AND M. L. DROSER. 1997. Nature and distribution of Cambrian shell concentrations: evidence from the Basin and Range Province of the western United States (California, Nevada, and Utah). *PALAIOS*, 12:111–126.
- LI, X., AND M. L. DROSER. 1999. Lower and Middle Ordovician shell beds from the Basin and Range province of the western United States (California, Nevada, and Utah). *PALAIOS*, 14:215–233.
- LU, P. J., M. YOGO, AND C. R. MARSHALL. 2006. Phanerozoic marine biodiversity dynamics in light of the incompleteness of the fossil record. *Proceedings of the National Academy of Sciences of the United States of America*, 103:2736–2739.
- LUPIA, R., S. LIDGARD, AND P. R. CRANE. 1999. Comparing palynological abundance and diversity: implications for biotic replacement during the Cretaceous angiosperm radiation. *Paleobiology*, 25:305–340.
- LUTZ, M. J., K. CALDEIRA, R. B. DUNBAR, AND M. J. BEHRENFELD. 2007. Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. *Journal of Geophysical Research: Oceans*, 112:C10011.
- MAKARIEVA, A. M., V. G. GORSHKOV, B.-L. LI, S. L. CHOWN, P. B. REICH, AND V. M. GAVRILOV. 2008. Mean mass-specific metabolic rates are strikingly similar across life's major domains: evidence for life's metabolic optimum. *Proceedings of the National Academy of Sciences*, 105:16994–16999.
- MANGANO, M. G., AND M. L. DROSER. 2004. The ichnologic record of the Ordovician radiation, p. 369–379. *In* B. D. Webby, F. Paris, M. L. Droser, and I. G. Percival (eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York.
- MARQUET, P. A., R. A. QUINONES, S. ABADES, F. LABRA, M. TOGNETTI, M. ARIM, AND M. RIVADENEIRA. 2005. Scaling and power-laws in ecological systems. *Journal of Experimental Biology*, 208:1749–1769.
- MARTIN, R. E. 1996. Secular increase in nutrient levels through the Phanerozoic: Implications for productivity, biomass, and diversity of the marine biosphere. *PALAIOS*, 11:209–219.
- MARTIN, R. E. 2003. The fossil record of biodiversity: nutrients, productivity, habitat area and differential preservation. *Lethaia*, 36:179–193.
- MCCLAINE, C. R. 2004. Connecting species richness, abundance and body size in deep-sea gastropods. *Global Ecology and Biogeography*, 13:327–334.
- MCCLAINE, C. R., A. P. ALLEN, D. P. TITTENSOR, AND M. A. REX. 2012. Energetics of life on the deep seafloor. *Proceedings of the National Academy of Sciences*, 109:15366–15371.
- MCCLAINE, C. R., A. G. BOYER, AND G. ROSENBERG. 2006. The island rule and the evolution of body size in the deep sea. *Journal of Biogeography*, 33:1578–1584.
- MCKINNEY, F. K., S. LIDGARD, J. J. SEPKOSKI, AND P. D. TAYLOR. 1998. Decoupled temporal patterns of evolution and ecology in two post-Paleozoic clades. *Science*, 281:807–809.
- MORAN, A. L., AND H. A. WOODS. 2012. Why might they be giants? Towards an understanding of polar gigantism. *The Journal of Experimental Biology*, 215:1995–2002.
- MORTON, B., AND K. CHAN. 1999. Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gastropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nassarius festivus* in Hong Kong. *Journal of Experimental Marine Biology and Ecology*, 240:213–228.
- NAGY, K. A. 2005. Field metabolic rate and body size. *Journal of Experimental Biology*, 208:1621–1625.
- NOVACK-GOTTSHALL, P. M. 2007. Using a theoretical ecospace to quantify the ecological diversity of Paleozoic and modern marine biotas. *Paleobiology*, 33:274–295.
- NOVACK-GOTTSHALL, P. M. 2008a. Using simple body-size metrics to estimate fossil body volume: Empirical validation using diverse Paleozoic invertebrates. *PALAIOS*, 23:163–173.
- NOVACK-GOTTSHALL, P. M. 2008b. Ecosystem-wide body size trends in Cambrian–Devonian marine invertebrate lineages. *Paleobiology*, 34:163–173.
- NÜTZEL, A., M. JOACHIMSKI, AND M. LÓPEZ-CORREA. 2010. Seasonal climatic fluctuations in the Late Triassic tropics—High-resolution oxygen isotope records from aragonitic bivalve shells (Cassian Formation, Northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 285:194–204.
- OJI, T., C. OGAYA, AND T. SATO. 2003. Increase of shell-crushing predation recorded in fossil shell fragmentation. *Paleobiology*, 29:520–526.
- PAULY, D. 2010. Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals. *Excellence in Ecology 22*, International Ecology Institute, Oldendorf/Luhe, Germany.
- PAYNE, J. L. 2005. Evolutionary dynamics of gastropod size across the end-Permian extinction and through the Triassic recovery interval. *Paleobiology*, 31:269–290.
- PAYNE, J. L., A. G. BOYER, J. H. BROWN, S. FINNEGAN,

- M. KOWALEWSKI, R. A. KRAUSE, S. K. LYONS, C. R. MCCLAIN, D. W. MCSHEA, P. M. NOVACK-GOTTSHALL, R. A. KRAUSE JR, F. A. SMITH, J. A. STEMPIEN, AND S. C. WANG. 2009. Two-phase increase in the maximum size of life over 3.5 billion years reflects biological innovation and environmental opportunity. *Proceedings of the National Academy of Sciences*, 106:24–27.
- PAYNE, J. L., AND S. FINNEGAN. 2006. Controls on marine animal biomass through geological time. *Geobiology*, 4:1–10.
- PAYNE, J. L., J. R. GROVES, A. B. JOST, T. NGUYEN, S. E. MOFFITT, T. M. HILL, AND J. M. SKOTHEIM. 2012. Late Paleozoic fusulinoidean gigantism driven by atmospheric hyperoxia. *Evolution*, 66:2929–2939.
- PAYNE, J. L., D. J. LEHRMANN, J. WEI, AND A. H. KNOLL. 2006. The pattern and timing of biotic recovery from the end-Permian extinction on the Great Bank of Guizhou, Guizhou Province, China. *PALAIOS*, 21:63–85.
- PAYNE, J. L., D. J. LEHRMANN, J. Y. WEI, M. J. ORCHARD, D. P. SCHRAG, AND A. H. KNOLL. 2004. Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science*, 305:506–509.
- PAYNE, J. L., C. R. MCCLAIN, A. G. BOYER, J. H. BROWN, S. FINNEGAN, M. KOWALEWSKI, R. A. KRAUSE, S. K. LYONS, D. W. MCSHEA, P. M. NOVACK-GOTTSHALL, F. A. SMITH, P. SPAETH, J. A. STEMPIEN, AND S. C. WANG. 2011. The evolutionary consequences of oxygenic photosynthesis: a body size perspective. *Photosynthesis Research*, 107:37–57.
- PAYTAN, A. 2009. Ocean paleoproductivity, p. 644–651. *In* V. Gornitz (ed.), *Encyclopedia of Paleoclimatology and Ancient Environments*. Springer, Berlin.
- PECK, L. S. 1992. Body volumes and internal space constraints in articulate brachiopods. *Lethaia*, 25:383–390.
- PECK, L. S. 1993. The tissues of articulate brachiopods and their value to predators. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 339:17–32.
- PETERS, S. E. 2004. Evenness of Cambrian–Ordovician benthic marine communities in North America. *Paleobiology*, 30:325–346.
- PETERS, S. E. 2005. Geologic constraints on the macroevolutionary history of marine animals. *Proceedings of the National Academy of Sciences of the United States of America*, 102:12326–12331.
- PETERS, S. E. 2006. Genus richness in Cambrian–Ordovician benthic marine communities in North America. *PALAIOS*, 21:580–587.
- PETERS, S. E. 2007. The problem with the Paleozoic. *Paleobiology*, 33:165–181.
- PETERS, S. E., AND N. A. HEIM. 2010. The geological completeness of paleontological sampling in North America. *Paleobiology*, 36:61–79.
- POWELL, E. N., G. M. STAFF, R. J. STANTON, AND W. R. CALLENDER. 2001. Application of trophic transfer efficiency and age structure in the trophic analysis of fossil assemblages. *Lethaia*, 34:97–118.
- POWELL, E. N., AND R. J. STANTON. 1985. Estimating biomass and energy-flow of mollusks in paleo-communities. *Palaeontology*, 28:1–34.
- POWELL, E. N., AND R. J. STANTON, JR. 1996. The application of size-frequency distribution and energy flow in paleoecologic analysis: An example using parautochthonous death assemblages from a variable salinity bay. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 124:195–231.
- POWELL, E. N., R. J. STANTON, JR., A. LOGAN, AND M. A. CRAIG. 1992. Preservation of Mollusca in Copano Bay, Texas. The long-term record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 95:209–228.
- PRICE, C. A., J. S. WEITZ, V. M. SAVAGE, J. STEGEN, A. CLARKE, D. A. COOMES, P. S. DODDS, R. S. ETIENNE, A. J. KERKHOFF, K. MCCULLOH, K. J. NIKLAS, H. OLFF, AND N. G. SWENSON. 2012. Testing the metabolic theory of ecology. *Ecology Letters*, 15:1465–1474.
- PRUSS, S. B., AND D. J. BOTTJER. 2004. Early Triassic trace fossils of the western United States and their implications for prolonged environmental stress from the end-Permian mass extinction. *PALAIOS*, 19:551–564.
- PRUSS, S. B., S. FINNEGAN, W. W. FISCHER, AND A. H. KNOLL. 2010. Carbonates in skeleton-poor seas: New insights from Cambrian and Ordovician strata of Laurentia. *PALAIOS*, 25:73–84.
- PRUSS, S., M. FRAISER, AND D. J. BOTTJER. 2004. Proliferation of Early Triassic wrinkle structures: Implications for environmental stress following the end-Permian mass extinction. *Geology*, 32:461–464.
- RAMEZANI, J., W. JIAYONG, P. ENOS, P. MONTGOMERY, J. L. PAYNE, M. J. ORCHARD, S. A. BOWRING, M. W. MARTIN, W. HONGMEI, AND D. J. LEHRMANN. 2006. Timing of recovery from the end-Permian extinction: Geochronologic and biostratigraphic constraints from south China. *Geology*, 34:1053–1056.
- REGO, B. L., S. C. WANG, D. ALTINER, AND J. L. PAYNE. 2012. Within-and among-genus components of size evolution during mass extinction, recovery, and background intervals: a case study of late Permian through Late Triassic foraminifera. *Paleobiology* 38:627–643.
- REX, M. A. 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology Progress Series*, 317:1.
- REX, M. A., J. A. CRAME, C. T. STUART, AND A.

- CLARKE. 2005. Large-scale biogeographic patterns in marine mollusks: a confluence of history and productivity? *Ecology*, 86:2288–2297.
- REX, M. A., R. J. ETTER, J. S. MORRIS, J. CROUSE, C. R. MCCLAIN, N. A. JOHNSON, C. T. STUART, J. W. DEMING, R. THIES, AND R. AVERY. 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology-Progress Series*, 317:1–8.
- RHODES, M. C., AND R. J. THOMPSON. 1993. Comparative physiology of suspension-feeding in living brachiopods and bivalves—evolutionary implications. *Paleobiology*, 19:322–334.
- RODLAND, D. L., AND D. J. BOTTJER. 2001. Biotic recovery from the end-Permian mass extinction: Behavior of the inarticulate brachiopod *Lingula* as a disaster taxon. *PALAIOS*, 16:95–101.
- ROY, K. 2002. Bathymetry and body size in marine gastropods: a shallow water perspective. *Marine Ecology Progress Series*, 237:143–149.
- ROY, K., D. JABLONSKI, AND K. K. MARTIEN. 2000. Invariant size-frequency distributions along a latitudinal gradient in marine bivalves. *Proceedings of the National Academy of Sciences of the United States of America*, 97:13150–13155.
- RUHL, H. A., J. A. ELLENA, AND K. L. SMITH. 2008. Connections between climate, food limitation, and carbon cycling in abyssal sediment communities. *Proceedings of the National Academy of Sciences*, 105:17006–17011.
- SAVAGE, V. M., E. J. DEEDS, AND W. FONTANA. 2008. Sizing up allometric scaling theory. *PLoS Computational Biology*, 4:e1000171.
- SAVAGE, V. M., J. F. GILLOOLY, J. H. BROWN, G. B. WEST, AND E. L. CHARNOV. 2004a. Effects of body size and temperature on population growth. *American Naturalist*, 163:429–441.
- SAVAGE, V. M., J. F. GILLOOLY, W. H. WOODRUFF, G. B. WEST, A. P. ALLEN, B. J. ENQUIST, AND J. H. BROWN. 2004b. The predominance of quarter-power scaling in biology. *Functional Ecology*, 18:257–282.
- SCHOUTEN, S., E. C. HOPMANS, AND J. S. SINNINGHE DAMSTÉ. 2013. The organic geochemistry of glycerol dialkyl glycerol tetraether lipids: A review. *Organic Geochemistry*, 54:19–61.
- SCHUBERT, J. K., AND D. J. BOTTJER. 1995. Aftermath of the Permian–Triassic mass extinction event—paleoecology of lower Triassic carbonates in the Western USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 116:1–39.
- SCHWINGHAMER, P., B. HARGRAVE, D. PEER, AND C. M. HAWKINS. 1986. Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. *Marine Ecology Progress Series*, 31:131–142.
- SEIBEL, B. A. 2007. On the depth and scale of metabolic rate variation: scaling of oxygen consumption rates and enzymatic activity in the Class Cephalopoda (Mollusca). *Journal of Experimental Biology*, 210:1–11.
- SEIBEL, B. A., AND J. C. DRAZEN. 2007. The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 362:2061–2078.
- SEPKOSKI, J. J., JR. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, 7:36–53.
- SEPKOSKI, J. J., JR. 1996. Competition in macroevolution: the double wedge revisited, p. 211–255. *In* D. H. Erwin, D. Jablonski, and J. H. Lipps (eds.), *Evolutionary Paleobiology*, University of Chicago Press, Chicago.
- SEPKOSKI, J. J., JR. 2002. A compendium of fossil marine animal genera. *Bulletins of American Paleontology*, 363:1–560.
- SEPKOSKI, J. J., R. K. BAMBACH, AND M. L. DROSER. 1991. Secular changes in Phanerozoic event bedding and the biological overprint, p. 299–312. *In* G. Einsele, W. Ricken, and A. Seilacher (eds.), *Cycles and Events in Stratigraphy*. Springer-Verlag, Berlin.
- SEPKOSKI, J. J., JR., AND A. I. MILLER. 1985. Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time, p. 153–190. *In* J. W. Valentine (ed.), *Phanerozoic Diversity Patterns: Profiles in Macroevolution*. Princeton University Press, Princeton, NJ.
- SEPKOSKI, J. J., JR., AND P. M. SHEEHAN. 1983. Diversification, faunal change, and community replacement during the Ordovician radiations, p. 673–718. *In* P. L. Tevesz and M. J. S. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum Press, New York.
- SHURIN, J. B., D. S. GRUNER, AND H. HILLEBRAND. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 273:1–9.
- SMITH, A. B., AND A. MCGOWAN. 2008. Temporal patterns of barren intervals in the Phanerozoic. *Paleobiology*, 34:155–161.
- SMITH, A. B., AND B. STOCKLEY. 2005. The geological history of deep-sea colonization by echinoids: roles of surface productivity and deep-water ventilation. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 272:865–869.
- STAFF, G., E. N. POWELL, R. J. STANTON, AND H. CUMMINS. 1985. Biomass: is it a useful tool in paleocommunity reconstruction? *Lethaia*, 18:209–232.
- STAFF, G. M., R. J. STANTON, JR., E. M. POWELL, AND H. CUMMINS. 1986. Time-averaging, taphonomy,

- and their impact on paleocommunity reconstruction: death assemblages in Texas bays. *Geological Society Of America Bulletin*, 97:428–443.
- SUN, Y., M. M. JOACHIMSKI, P. B. WIGNALL, C. YAN, Y. CHEN, H. JIANG, L. WANG, AND X. LAI. 2012. Lethally hot temperatures during the Early Triassic Greenhouse. *Science*, 338:366–370.
- TAPPAN, H. 1982. Extinction or survival: selectivity and causes of Phanerozoic crises. *Geological Society of America Special Papers* 190:265–276.
- TAPPAN, H. 1986. Phytoplankton: below the salt at the global table. *Journal of Paleontology*, 60:545–554.
- THAYER, C. W. 1983. Sediment-mediated biological disturbance and the evolution of marine benthos, p. 480–595. *In* M. J. S. Tevesz and P. L. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum Press, New York.
- THAYER, C. W. 1986. Are brachiopods better than bivalves? Mechanisms of turbidity tolerance and their interaction with feeding in articulates. *Paleobiology*, 12:161–174.
- TOMAŠOVÝCH, A., AND S. M. KIDWELL. 2009. Preservation of spatial and environmental gradients by death assemblages. *Paleobiology*, 35:119–145.
- TOMAŠOVÝCH, A., AND J. N. SCHLÖGL. 2008. Analyzing variations in cephalopod abundances in shell concentrations: The combined effects of production and density-dependent cementation rates. *PALAIOS*, 23:648–666.
- TRIBOVILLARD, N., ALGEO, T., LYONS, T., AND RIBOULLEAU, A. 2006. Trace metal proxies for paleoredox and paleoproductivity. *Chemical Geology*, 232: 12–32.
- TWITCHETT, R. J. 2007. The Lilliput effect in the aftermath of the end-Permian extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 252:132–144.
- URBANEK, A. 1993. Biotic crises in the history of upper Silurian graptoloids: a paleobiological model. *Historical Biology*, 7:29–50.
- VALENTINE, J. W. 1971. Resource supply and species diversity patterns. *Lethaia*, 4:51–61.
- VALENTINE, J. W. 1973. *Evolutionary Paleoecology of the Marine Biosphere*. Prentice Hall, Englewood Cliffs, New Jersey.
- VALENTINE, J. W., AND E. M. MOORES. 1970. Plate-tectonic regulation of faunal diversity and sea level: a model. *Nature*, 228:657–659.
- VAN DE SCHOOTBRUGGE, B., T. BAILEY, Y. ROSENTHAL, M. KATZ, J. D. WRIGHT, S. FEIST-BURKHARDT, K. G. MILLER, AND P. G. FALKOWSKI. 2005. Early Jurassic climate change and the radiation of organic-walled phytoplankton in the Tethys Ocean. *Paleobiology*, 31:73–97.
- VAN DE SCHOOTBRUGGE AND S. GOLLNER. 2013. Altered primary production during mass-extinction events, p. 87–114. *In* A. M. Bush, S. B. Pruss, and J. L. Payne (eds.), *Ecosystem Paleobiology and Geobiology, The Paleontological Society Papers* 19. Yale Press, New Haven.
- VAN VALEN, L. 1976. Energy and evolution. *Evolutionary Theory*, 1:179–229.
- VERMEIJ, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, 3:245–258.
- VERMEIJ, G. J. 1987. *Evolution and Escalation: An Ecological History of Life*. Princeton University Press, Princeton, New Jersey.
- VERMEIJ, G. J. 1995. Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology*, 21:125–152.
- VERMEIJ, G. J. 2002. Evolution in the consumer age; predators and the history of life, p. 75–393. *In* M. Kowalewski and P. H. Kelley (eds), *The Fossil Record of Predation. The Paleontological Society Papers* 8, Yale Press, New Haven.
- VERMEIJ, G. J. 2004. *Nature: An Economic History*. Princeton University Press, Princeton, New Jersey.
- VLADIMIROVA, I. G. 2001. Standard metabolic rate in Gastropoda class. *Biology Bulletin*, 28:163–169.
- VLADIMIROVA, I. G., S. Y. KLEIMENOV, AND L. I. RADZINSKAYA. 2003. The relation of energy metabolism and body weight in bivalves (Mollusca: Bivalvia). *Biology Bulletin of the Russian Academy of Sciences*, 30:392–399.
- WAGNER, P. J., M. A. KOSNIK, AND S. LIDGARD. 2006. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. *Science*, 314:1289–1292.
- WARWICK, R. M., AND K. R. CLARKE. 1996. Relationships between body-size, species abundance and diversity in marine benthic assemblages: Facts or artefacts? *Journal of Experimental Marine Biology and Ecology*, 202:63–71.
- WEI, C.-L., G. T. ROWE, E. ESCOBAR-BRIONES, A. BOETIUS, T. SOLTWEDEL, M. J. CALEY, Y. SOLIMAN, F. HUETTMANN, F. QU, AND Z. YU. 2010. Global patterns and predictions of seafloor biomass using random forests. *PLoS ONE*, 5:e15323.
- WEI, C.-L., G. T. ROWE, E. ESCOBAR-BRIONES, C. NUNNALLY, Y. SOLIMAN, AND N. ELLIS. 2012. Standing stocks and body size of deep-sea macrofauna: Predicting the baseline of 2010 *Deepwater Horizon* oil spill in the northern Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers*, 69:82–99.
- WEST, G. B. 2002. Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 99:2473–2478.
- WEST, G. B., J. H. BROWN, AND B. J. ENQUIST. 1997. A

- general model for the origin of allometric scaling laws in biology. *Science*, 276:122–126.
- WEST, G. B., V. M. SAVAGE, J. GILLOOLY, B. J. ENQUIST, W. H. WOODRUFF, AND J. H. BROWN. 2003. Why does metabolic rate scale with body size? *Nature*, 421:713.
- WESTROP, S. R., J. V. TREMBLAY, AND E. LANDING. 1995. Declining importance of trilobites in Ordovician nearshore paleocommunities—dilution or displacement? *PALAIOS*, 10:75–79.
- WHITE, C. R., P. CASSEY, AND T. M. BLACKBURN. 2007. Allometric exponents do not support a universal metabolic allometry. *Ecology*, 88:315–323.
- WITMAN, J. D., AND K. ROY. 2009. *Marine Macroecology*. University of Chicago Press. Chicago.
- ZARDINI, R. 1978. *Fossili Cassiani (Trias Medio-Superiore): Atlante dei gasteropodi della formazione di S. Cassiano raccolti nella regione Dolomitica attorno a Cortina d'Ampezzo*. Edizioni Ghedina, Cortina d'Ampezzo.

