Controls on marine animal biomass through geological time

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ABSTRACT

Total animal biomass depends on four factors: (1) food supply, (2) the efficiency with which animals consume available food, (3) the efficiency with which animals convert consumed food into biomass, and (4) the rate at which animals lose biomass to the environment through respiration or death. Each of these factors may change through geological time because each is a function of animal ecology and physiology. Animal ecology and physiology, in turn, are products of interacting evolutionary and environmental factors. The direction of change in animal biomass through time may be predicted given knowledge of environmental and ecological change. At a finer level, physiological differences among phyla or other higher taxa suggest that they would have had differential responses to specific environmental changes. Physiological features shared by all of life, such as the dependence of metabolic rate on ambient temperature, suggest that even a coarse time-series of relative changes in animal biomass may enrich understanding of biogeochemical cycling among all organisms, including phytoplankton and microbes. Changes in the abundance of skeletal material in shallow marine deposits through geological time indicate that the biomass of benthic skeletal invertebrates has fluctuated significantly on timescales from millions to hundreds of millions of years. During the Ordovician radiation, increase in the complexity of animal food webs and increase in the efficiency of animal communities in removing available food from the water column and sediment appear most likely to account for a secular increase in animal biomass. Decrease in animal biomass after the end-Permian extinction appears to have been driven by a combination of factors but particularly decreased aggregate growth efficiency and consumption efficiency. Comparing biomass and diversity trends through other major transitions in the history of animal life has the potential to shed light on the relationship between physical environmental change and ecosystems evolution.

INTRODUCTION

The Phanerozoic history of animal diversity in the marine realm is well characterized (Sepkoski *et al.*, 1981; Sepkoski, 1993, 2002; Benton, 1995), and although debate continues over the pattern of diversity change (see, e.g. Alroy *et al.*, 2001; Bush & Bambach, 2004b; Peters, 2005) and the fundamental drivers of diversity trends (Adrain & Westrop, 2000; Smith, 2001; Peters & Foote, 2002; Jablonski *et al.*, 2003; Bush & Bambach, 2004b; Kidwell, 2005b; Peters, 2005), the diversity curve has held its basic shape for well over a century (see, e.g. Phillips, 1860).

In contrast, the history of animal abundance in the marine realm (or the terrestrial realm for that matter) remains almost entirely unconstrained both in terms of the number of individual organisms present and in terms of the total biomass or standing energy represented by those organisms. Attempts to quantify changes in biomass on a global scale through geological time have focused primarily on total biomass of all life (e.g. Van Valen, 1976; Benton, 1979; Schidlowski, 1991). Prior to the evolution of oxygenic photosynthesis it is agreed that primary production was substantially limited by available reducing power (Benton, 1979; Schidlowski, 1991). Assessments of the trajectory of total biomass since the advent of oxygenic photosynthesis during the late Archean (Brocks *et al.*, 1999) fall into two camps: constant biomass and increasing biomass. The constant biomass argument relies primarily on the fact that even microbial communities utilize nearly all available nutrients and, thus, have been nutrient limited through time (Schidlowski, 1991). However, expansion of life from sea to land and the subsequent storage of large quantities of biomass in terrestrial forests may have resulted in increased biomass by allowing access to previously unavailable nutrients (Benton, 1979) that may in turn have been cycled into marine ecosystems. Also,

increased oxygen content in seawater and increased levels of bioturbation may have reduced the efficiency of organic matter burial, thus increasing the nutrient load, productivity, and animal biomass in the water column (Schopf, 1980; Thayer, 1983).

Animal biomass, even if limited to the marine realm, is more difficult to constrain from a theoretical standpoint than the biomass of primary producers because the complexity of animal food webs leaves open the possibility that animal biomass does not have any simple relationship to available food supply. Total animal biomass must have increased since the origin of the first animals at some point during the Proterozoic and it is likely that total marine animal biomass has continued to change since the Cambrian. Increases in nutrient availability and primary productivity are hypothesized to have fuelled increased animal diversity and total biomass in the marine realm through the Phanerozoic (see, e.g. Bambach, 1993, 1999; Vermeij, 1995; Martin, 2003; Katz et al., 2004). Available data on the abundance and thicknesses of shell beds through time and the abundance of skeletal grains in shallow marine carbonate strata suggest that fluctuations in the biomass of skeletal benthic marine invertebrates may have been quite dramatic (Kidwell & Brenchley, 1994, 1996; Li & Droser, 1999; Payne et al. in press). Although greater durability of shells with low-organic microstructure and increased occupation of high energy shoreface and shoal environments through time have clearly played a role in the secular increase in thickness of shell beds through the Phanerozoic (Kidwell & Brenchley, 1996), increasing rates of skeletal production are also likely to have been important factors (e.g. Kidwell & Brenchley, 1996). Recent work demonstrating comparable scales of time averaging in bivalve and brachiopod shell beds lends greater credibility to shell beds as records of animal abundance (Carroll et al., 2003; Kidwell, 2005a).

These observations highlight the large number of questions that can only be addressed with information on animal abundance through the Phanerozoic. How much has the biomass of marine animals varied through the Phanerozoic? How have secular trends in nutrient flux impacted animal biomass? How have global tectonic and climatic cycles affected the amount and distribution of biomass? Have evolutionary radiations increased overall biomass by tapping into previously underutilized resources, or have they merely subdivided a constant resource pool more finely? Have changes in biomass paralleled changes in diversity? Although taxonomic diversity has been used as a proxy for biomass (e.g. Rothman, 2001), the relationship between these two variables is complex in modern ecosystems (Waide et al., 1999; Mittelbach et al., 2001) and is unknown in ancient ones. Because total biomass cannot be compiled in the same way that total diversity can (i.e. it is impossible to count the total number or volume of known fossils on Earth for a given time interval), more indirect proxies are required. Interpreting such proxy records, however, also requires a clear understanding of the relationships between proxies and total marine animal biomass.

Quantification of animal biomass through the Phanerozoic would also constrain hypotheses regarding feedbacks between the Earth system and the evolution of life. The fossil record of animals, particularly of skeletal benthic marine invertebrates, has temporal, spatial, and taxonomic resolution at a scale unavailable for terrestrial plants and animals or for marine phytoplankton (particularly in the Palaeozoic). Although only a fraction of marine invertebrate taxa have mineralized skeletons, comparison of exceptional fossil deposits preserving soft-bodied forms with modern benthic communities reveals no obvious trend in the fraction of taxa with preservable skeletons (see, e.g. Bambach, 1977; Conway Morris, 1986) or the fraction of biomass contributed by the well preserved taxa (see Conway Morris, 1986). Data recording changes in biomass are essential because nutrient cycling depends not only on the available metabolic pathways but also – critically – on the flux through each of those pathways. Because animals are extremely similar in their nutrient demands (Sterner & Elser, 2002), fine-scale taxonomic resolution is not required to understand the effects of changing nutrient cycling on animal biomass (or vice versa). Furthermore, many general physiological and ecological scaling relationships hold across phyla and for organisms differing in size by many orders of magnitude (see, e.g. Peters, 1983; Schmidt-Nielsen, 1984; Cossins & Bowler, 1987; Brown, 1995; Gillooly et al., 2001a,b; Savage et al., 2004). Substantial variation of community biomass on ecological timescales is suggested by observation and modelling and can be explained in large part by physiological correlates of body size and temperature (Allen et al., 2005). Some basic physiological attributes are shared even between animals and microbes (e.g. dependence of metabolic rate on external temperature). Therefore, inferences from the animal fossil record may, in some cases, be applicable to more poorly preserved prokaryotes and unicellular eukaryotes. A satisfactory understanding of biogeochemical cycling requires not only a complete inventory of the metabolic pathways available to life, but also a history of the fluxes of matter that have passed through those various pathways. A quantitative record of animal biomass can help to outline this history.

At the scales of individual organisms and of global ecosystems, changes in biomass reflect changes in the amount of available food taken up from the environment and retained as tissue mass. Thus, increases in nutrient supply and primary productivity are often proposed to explain increases in animal size, biomass, and inferred metabolic rate in the fossil record (see, e.g. Bambach, 1993, 1999; Vermeij, 1995; Martin, 1996, 2003; Katz et al., 2004). Quantitative models developed to understand the dynamics of biomass distribution in modern food webs (e.g. Kerr & Dickie, 2001; Allen et al., 2005) generally have not been extended to the study of ecosystem development on geological/evolutionary timescales. Adapting this framework to address the fossil record, however, makes clear not only that a variety of factors influence marine animal biomass but also that a variety of observations can be

used to constrain the fossil record in this light. There are four broad classes of factors that affect the standing pool of animal biomass.

Primary productivity (*P*)

Primary productivity is controlled by the rate of nutrient delivery, the nutrient demands of primary producers, and the efficiency with which they are able, in aggregate, to convert nutrients into biomass. Over timescales of 10^6 years or more, primary productivity is nutrient limited, either by the supply of phosphorus or trace-metal nutrients from weathering (e.g. Van Cappellen & Ingall, 1994; Watson *et al.*, 2000) or by nitrogen fixation (Falkowski, 1997). Therefore, long-term secular trends in nutrient availability should reflect controls on either nutrient delivery from weathering or controls on the rate of nitrogen fixation. Nutrient delivery is controlled by rates of mineral supply from tectonic uplift and chemical weathering of available minerals (e.g. West *et al.*, 2005). Thus, tectonic or climatic factors may limit weathering rates at different times and locations. Oceanographic changes such as increased upwelling or more effective phosphorus regeneration under anoxic conditions (Van Cappellen & Ingall, 1994) may also affect primary productivity through changes in the pattern and timing of nutrient supply. Under conditions where primary production is nitrogen-limited, the availability of trace metal nutrients required for nitrogen fixation may also be instrumental in setting the rate of primary production (Anbar & Knoll, 2002; Jickells *et al.*, 2005).

Consumption efficiency (*c*)

The efficiency of animal consumption, in turn, depends on the spatial and temporal distribution of primary production, as well as the proportion of primary production palatable to animal consumers. Many primary producers inhibit consumers by the production of toxins, the secretion of a hard shell, or by population blooms that occur too rapidly for consumers to respond effectively. Guild structure in local communities and on a global scale is likely to affect the efficiency with which animals, in aggregate, are able to consume available food resources. Secular increases in community-level diversity (Bambach, 1977) and in the number of ecotypes represented within marine communities through the Phanerozoic (Bush & Bambach, 2004a) suggest that, in aggregate, animal communities have become more efficient in gathering available food resources. Likewise, expanded epifaunal and infaunal tiering (Ausich & Bottjer, 1982; Bottjer & Ausich, 1986) may reflect a general increase in consumption efficiency since the Cambrian. However, predators can limit the biomass of primary consumers, potentially providing a stabilizing feedback between diversity and biomass within communities. The proportion of marine diversity represented by predators has, in fact, increased through the Phanerozoic (Bambach *et al.*, 2002), although it is not necessary that their proportional biomass has changed in parallel.

Growth efficiency (*g*)

A variety of physiological factors affect the growth efficiency of animal consumers. Growth efficiency in animals (and all other organisms) is strongly correlated with temperature. Organisms tend to grow less efficiently at higher temperatures due to elevated respiratory demands (Cossins & Bowler, 1987; Brown *et al.*, 2004). Growth efficiency is also a function of physiology and ecology, factors that vary among high-level taxonomic groups. The best-known example of this phenomenon is the difference between homeotherms (i.e. warm-blooded organisms) and poikilotherms (i.e. cold-blooded organisms). Homeotherms have much higher metabolic rates due to the energetic demands of maintaining a constant body temperature in the face of fluctuating external conditions (Cossins & Bowler, 1987). A more relevant example from the marine realm is the contrast in metabolic rate between two of the most abundant clades in the fossil record: brachiopods and bivalves. Bivalves have much higher average per gram metabolic rates than brachiopods and their relative abundance in shallow marine communities has increased over the course of the Phanerozoic while the relative abundance of brachiopods has decreased (Rhodes & Thompson, 1993). A related trend, the stepwise increase in proportion of motile organisms through the Phanerozoic, also implies an increase in average metabolic rate due to the energetic demands of locomotion (Bambach *et al.*, 2002). Because all of these factors affect growth efficiency, major climatic shifts or major changes in the taxonomic composition and ecological structure of animal communities, particularly of the primary consumers, should have strong effects on the capacity of primary productivity to support animal biomass.

Residence time (*k*)

In addition to controls on animal growth, changes in rates of death and respiration also affect standing biomass. Larger organisms have longer lifespans and lower specific (i.e. per gram) metabolic rates than smaller organisms (e.g. Schmidt-Nielsen, 1984). As a result, an increase in the number or proportion of large organisms would increase standing biomass by decreasing the per gram rates of death and respiration. Therefore, the distribution of body sizes in marine communities can be used as a proxy for the residence time of biomass in the animal pool. Other than size, perhaps the most critical factor affecting the loss rate of animal biomass is the structure of animal food webs. Some animal biomass remains within animal communities when primary consumers are eaten by predators. Thus, the addition of mid-level and top predators to animal communities can also increase the residence time of biomass within the animal

community, particularly because predators tend to be large and long-lived.

A CONCEPTUAL MODEL

Below we formalize the relationships described above in a simple conceptual model. The value of such a model lies not in determining precise parameter values, but rather in gaining a more complete understanding of how various factors are involved in controlling total biomass of animal communities. The model is equally applicable to the biomass of any community, including bacteria, land plants, algae, or life as a whole.

Changes in animal biomass occur when the rate at which new animal biomass is formed via growth does not equal the rate at which existing animal biomass is lost due to death and respiration. This is true for individual animals and also for global animal biomass, which is the sum of many individual organisms, and can be expressed mathematically as:

$$dB/dt = F_{in} - F_{out}, \qquad (1)$$

where dB/dt is the rate of change of biomass with respect to time, F_{in} is the flux of biomass into the animal pool (i.e. rate of growth) and F_{out} is the flux of biomass out of the living animal pool due to death and respiration.

It is possible to be more specific in defining the flux terms by stipulating a few basic conditions and relationships:
1 All animal food derives (ultimately) from primary productivity, termed P.
2 The proportion of primary productivity that becomes animal biomass is controlled by the proportion of primary productivity that is eaten by animals (*consumption efficiency*), termed c.
3 The proportion of primary productivity that becomes animal biomass is also controlled by the proportion of what is eaten that is converted to biomass rather than being respired or egested. The *growth efficiency* is termed g.
4 A simple model for the loss of animal biomass holds that it is proportional to the standing biomass. In other words, in the absence of primary production, animal biomass would decrease exponentially as animals continued to respire and eventually died. The residence time is termed k, and standing animal biomass is termed B.

These relationships can be used to modify equation 1 as follows:

$$dB/dt = cgP - B/k. \qquad (2)$$

Equation 2 can be thought of as a modified version of the well-known Lotka–Volterra equations used to describe population dynamics between predators and prey. There is only a single expression in this case, rather than multiple equations, because primary productivity (P) is assumed, for simplicity, to be independent of animal biomass (B).

As discussed above, many complex ecological phenomena affect the values of these few parameters. Given these complexities, this simple formulation facilitates conceptual and quantitative assessment of the effects of changes in ecological and biogeochemical systems on animal biomass. Adequate data could permit further separation of the controlling parameters but a simple formulation seems the best place to start.

Using this model, it is possible to predict the effects of climatic and ecological changes observable in the rock record on the other factors that also affect the total biomass of marine animals. The expected response of animal biomass to changes in environmental parameters such as climate or ecological parameters such as body size and habitat area can then be tested against patterns observed in the fossil record.

DISCUSSION

How well can the conceptual model be applied to the fossil record? Whereas the noise introduced by the uneven palaeogeographical and environmental representation of the rock record, taphonomic filtering, and changes in the proportion of animals that produce preservable hard parts may obscure the primary signal in many instances, dramatic short-term and long-term changes in skeletal abundance do appear to leave a recognizable signature in the rock record (e.g. Kidwell & Brenchley, 1996; Li & Droser, 1999; Kidwell, 2005a; Payne *et al.*, in press). Below we address two examples of intervals where observation of the fossil record suggests a substantial change in animal biomass within marine benthic communities – at least of the skeletal animals. In each case primary evidence comes from measurable changes in fossil abundance determined through volumetric analysis or compilation of the abundance and thicknesses of shell beds. It is assumed that the abundance of skeletal remains can serve as a first-order proxy for the abundance of skeletal animals. This assumption can be tested on a case-by-case basis to determine whether depositional, taphonomic, environmental, or evolutionary factors might better account for observed changes in fossil abundance. During the Cambrian radiation, for example, it is unlikely that the proportion of animal biomass consisting of skeletal individuals remained constant. The ratio of soft-tissue mass to skeletal mass is also assumed to be constant across higher taxa and constant within higher taxa across large size ranges. This assumption can be relaxed using relevant observations of living organisms. The first example is a temporary decrease in marine benthic animal biomass across the end-Permian mass extinction and the second a long-term increase during the Ordovician radiation.

End-Permian extinction

Several lines of evidence indicate that the taxonomically severe end-Permian mass extinction also reduced the abundance of marine benthic animals. First, Lower Triassic strata around the

globe are characterized by reduced bioturbation indicating a low density of burrowing animals (Twitchett, 1999; Pruss & Bottjer, 2004; Pruss *et al.*, 2004). Further support for a low biomass scenario is provided by qualitative observations of reduced fossil abundance above the extinction horizon on low latitude carbonate ramps (Baud *et al.*, 1997) and in higher latitude siliciclastic deposits (Twitchett *et al.*, 2001). Reduced animal abundance has been called upon to explain the absence of some genera surviving the extinction from the Lower Triassic rock record (Wignall & Benton, 1999) and the generally small size of those taxa found in Lower Triassic strata (Twitchett, 2001).

Quantitative support for reduced animal biomass comes from direct determination of the abundance of fossil grains in Permian–Triassic strata of an isolated carbonate platform – the Great Bank of Guizhou – in southern China. Payne *et al.* (in press) determined the volume of animal (and algal) skeletal grains on the platform as a fraction of rock volume by point-counting 349 thin sections of samples from the Upper Permian through the Middle Triassic. Skeletal volume decreased by more than an order of magnitude across the Permian–Triassic boundary in all sampled environments, ranging from shallow platform interior settings to deeper water on the adjacent basin margin. It is difficult to account for the observed decrease in skeletal abundance exclusively by rock-record biases because the decrease is so pronounced. Rather, a decrease in the biomass of benthic skeletal organisms during the Early Triassic is likely to account, at least in part, for decreased skeletal abundance. Figure 1A illustrates the percent of rock volume represented by animal, algal, and foraminiferal clasts in the basin margin environment from the Late Permian through the Middle Triassic. Fossil abundance remained low through most of the Lower Triassic (approximately 3 million years) before increasing in the Spathian (latest Early Triassic) and Anisian (earliest Middle Triassic) (Fig. 1A).

Several lines of evidence indicate that in this locality the abundance of skeletal carbonates as a fraction of rock volume can serve as a reasonable proxy for the biomass of skeletal benthic organisms. First, backstripping analysis of the Nanpanjiang Basin (Christensen & Lehrmann, 2004) demonstrates that sedimentation rates on the platform were relatively constant through the study interval, not varying by more than a factor of two or three at stage timescales. Second, the exposure of a two-dimensional cross-section of the platform by a steeply dipping faulted syncline allows comparison of skeletal abundance across environments from platform interior to basin margin. Third, although Lower Triassic fossils are generally small and aragonitic, they are preserved in strata containing ooids and precipitated microbialites, suggesting that postmortem dissolution of carbonate shells was less common than penecontemporaneous carbonate precipitation and therefore unlikely to overwhelm the primary biological signal. Ideally, of course, each of these factors – depositional, environmental, and preservational – would be better constrained. To a first
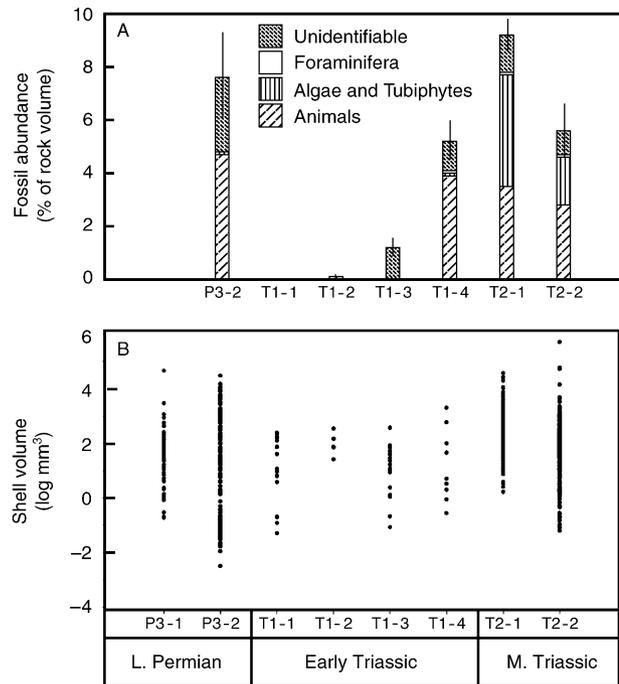

Fig. 1 Data indicating decreased animal biomass across the Permian–Triassic boundary and increased biomass from the Early to Middle Triassic. (A) Abundance of fossil grains from the Guandao section on the Great Bank of Guizhou, China. Vertical black lines indicate one standard deviation of the mean skeletal content. From Payne *et al.* (in press). (B) Compilation of the sizes of all gastropod species globally from the Late Permian through the Middle Triassic collected from the published literature. Each dot represents one species occurrence – type specimens were selected whenever possible. See Payne (2005) for methodological details. From Payne (2005). (P3-1 – Djulfian; P3-2 – Changhsingian; T1-1 – Griesbachian; T1-2 – Dienerian; T1-3 – Smithian; T1-4 – Spathian; T2-1 – Anisian; T2-2 – Ladinian).

order, however, they suggest that the local record is likely to be as faithful as could be hoped for in the rock record.

If evidence for decreased abundance of benthic invertebrates during the Early Triassic is reliable, what were the likely drivers of such a decrease? Environmental stresses such as persistent shallow marine dysoxia (Hallam, 1991; Wignall & Twitchett, 2002) may have played a role in limiting available habitat space and continuing environmental disturbance may be reflected in instability of the Early Triassic carbon cycle (Payne *et al.*, 2004). However, the low density of skeletal benthic invertebrates on the Great Bank of Guizhou, where there is little evidence for dysoxia in shallow water settings, suggests oxygen was not the only important control on animal abundance. Primary productivity has been called upon previously as the most important control (Twitchett, 2001). On a global scale, primary productivity is likely to be limited by the availability of nutrients such as phosphorus (Van Cappellen & Ingall, 1994), nitrogen (Falkowski, 1997), or iron (e.g. Watson *et al.*, 2000). Substantial climate change across the Permian–Triassic boundary (Retallack, 1999) could have impacted nutrient delivery through effects on weathering rate

and/or ocean circulation. Low levels of bioturbation during the Early Triassic (Twitchett, 1999; Pruss & Bottjer, 2004) could have increased the burial efficiency of organic carbon and, consequently, decreased the proportion of nutrients recycled into the water column (*sensu* Thayer, 1983). Widespread anoxia at this time, however, would be expected to increase the efficiency of phosphate recycling (Van Cappellen & Ingall, 1994). Overall, primary productivity is quite difficult to constrain. Evidence that other factors played a role in changing the biomass of marine benthic animals is stronger. Reduced epifaunal and infaunal tiering (Bottjer & Ausich, 1986; Twitchett *et al.*, 2004) and reduced bioturbation (Twitchett, 1999; Pruss & Bottjer, 2004; Pruss *et al.*, 2004) indicate that available food was less likely to enter the mouths of benthic invertebrates before and after it reached the sediment surface resulting in reduced consumption efficiency. The aggregate growth efficiency of marine benthic invertebrates is also likely to have changed substantially across the Permian–Triassic boundary. Bivalves and gastropods, by far the most abundant members of Early Triassic marine benthic communities (Schubert & Bottjer, 1995; Payne *et al.*, in press), have higher respiration rates and lower growth efficiencies than brachiopods and echinoderms, dominant components of Late Permian communities. Given an equal food supply, Early Triassic mollusks could not have lived at the same density as Late Permian brachiopods. This effect would be exacerbated by increased temperatures during the Early Triassic (Retallack, 1999) due to the temperature dependence of respiration rate (e.g. Schmidt-Nielsen, 1984). Furthermore, there is evidence of a substantial increase in the proportion of primary productivity contributed by cyanobacteria in the immediate aftermath of end-Permian extinction (Xie *et al.*, 2005). Experimental evidence suggests that cyanobacteria are a less effective source of food for invertebrates than many eukaryotic algae, in part due to their lack of sterols used by the invertebrates in the biosynthesis of cholesterol (von Elert *et al.*, 2003). Finally, reduction in the maximum size of marine benthic invertebrates (Twitchett, 2001; Fraiser & Bottjer, 2004; Payne, 2005) would have decreased the average residence time of organic carbon in animals (k) because smaller organisms have higher per gram metabolic rates than larger organisms. Figure 1(B) illustrates the sizes of all known gastropod species globally from the Late Permian through the Middle Triassic compiled from the published literature by Payne (2005), demonstrating that the interval lacking large species globally coincides with the interval characterized by low fossil abundance on the Great Bank of Guizhou. Subsampling indicates that the change in maximum size is not merely due to the smaller number of described Early Triassic species (Payne, 2005). Unfortunately, change in mean size is much more difficult to determine with statistical confidence than change in maximum size because small gastropod species tend to be sampled less effectively than larger species and description of the smallest taxa (< 2 mm in height) tends to be confined to exceptionally preserved deposits

during this interval (see discussion in Payne, 2005). Apparent changes in mean size may be strongly dependent on changes in the number of exceptional deposits and the number of known small species.

In summary, it is possible that all of the primary controls on animal biomass – food supply, consumption efficiency, growth efficiency, and turnover rate – were substantially altered in the Early Triassic. Observations of the Early Triassic fossil record of benthic invertebrates suggest that low diversity ecosystems may tend to support less biomass than higher diversity ecosystems – a scenario clearly requiring further empirical and theoretical testing.

The Ordovician radiation

Aside from the increase implied by the five-fold expansion of marine genus diversity during the Ordovician radiation (Sepkoski, 2002), several sets of data offer more direct evidence of increased animal biomass through the Ordovician Period. The depth and intensity of bioturbation increased dramatically (Droser & Bottjer, 1989) signalling an increase in infaunal animal biomass. The frequency and thickness of shell beds in the Lower and Middle Ordovician of the Great Basin of the USA suggests an increase in the total abundance of skeletonized animals (Li & Droser, 1997, 1999). Increases in average body size occurred in rhynchonelliform and linguliform brachiopods (Jin, 2001; Stempien & Kowalewski, 2002; Harper *et al.*, 2004) and possibly trilobites (Churchill-Dickson, 2001; Rudkin *et al.*, 2003). Similar trends of increasing body size are likely to characterize other clades as well (Novack-Gottshall, 2005).

Increase in body size does not necessarily imply increased biomass, given the expected negative correlation between body size and population density (Damuth, 1987). Abundance data must also be analysed, and such data are rarely available. Figure 2 presents body size, relative abundance, and total biovolume of rhynchonelliform brachiopods in a compilation of local community samples from Laurentian mixed carbonate-clastic depositional environments. Although relative abundance data must be interpreted cautiously (Finnegan & Droser, 2005) there is little doubt that the absolute abundance of rhynchonelliform brachiopods increased during the Ordovician (Harper, in press), and so relative abundance data may be used to estimate general trends in population density of this clade.

There is a clear and substantial increase in the total community-level biovolume of brachiopods in this sample set. This trend in complicated by environmental heterogeneity – Lower and Middle Ordovician data come exclusively from carbonate ramp and platform environments in the western USA, while Upper Ordovician data come from foreland basin and cratonic environments in the eastern USA. These environments may have received considerably higher nutrient inputs (Pope & Steffen, 2003), and it has been suggested
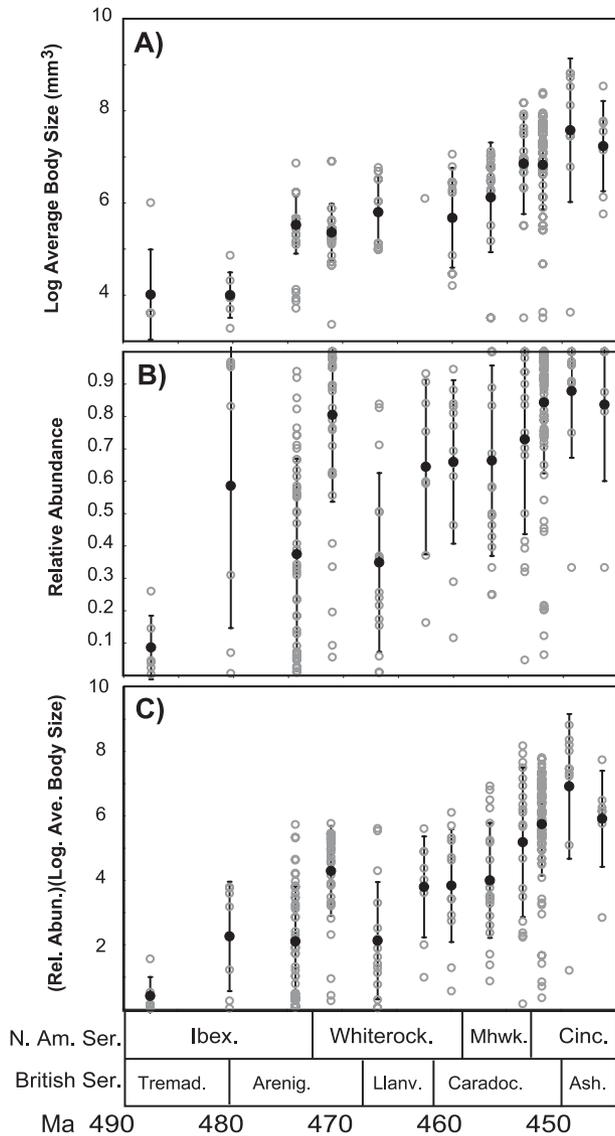
Fig. 2 Data indicating increasing brachiopod biomass through the Ordovician. (A) Average body size of rhynchonelliform brachiopod species in 311 samples from low-latitude Ordovician carbonates. (B) Relative abundance of brachiopods in the same samples. (C) Average body size multiplied by relative abundance as a measure of total brachiopod biovolume. Filled circles represent means of all samples for a given time interval and the error bars represent one standard deviation around the mean. Body volumes are simple geometrical approximations based on direct measurements of individuals in samples and museum collections. Ibexian and Whiterockian samples are from the Basin and Range region of the western USA (S. Finnegan, unpublished data), Mohawkian and Cincinnatian samples are from the eastern USA (compiled from the published literature and from the Palaeobiology Database). Ibex. = Ibexian, Whiterock = Whiterockian, Mhwk. = Mohawkian, Cinc. = Cincinnatian, Tremad. = Tremadocian, Arenig. = Arenigian, Llanv. = Llanvirnian, Caradoc. = Caradocian, Ash. = Ashgillian.

that, for some groups, average body sizes are larger in cratonic seaways (Jin, 2001). However, the most striking increases in abundance, body size, and total biovolume occur within these two intervals, rather than between them, suggesting

that the overall trend is not driven by differences in environmental representation.

There are also numerous lines of indirect evidence which suggest that the standing biomass of animals increased during the Ordovician Period. Available habitat area grew on continental shelves and in epeiric seas as sea level rose to the Phanerozoic highstand. Although size increase seems to be a general trend through the Ordovician, it is particularly pronounced in cratonic seas (Jin, 2001), and expansion of these habitats may have amplified the observed trend. Enhanced early lithification of hardgrounds – perhaps driven by low Mg/Ca ratios – also expanded opportunities for many sessile taxa (Guenberg & Sprinkle, 1992; Palmer & Wilson, 2004). Substantial increases in trace-fossil diversity are also seen in deep marine settings and marginal marine environments (Orr, 2001; Mangano & Droser, 2004). The increased complexity of marine ecosystems almost certainly increased the standing energy of the marine biota (Bambach, 1983, 1993) and suggests an increase in the aggregate consumption efficiency of benthic marine communities at this time.

Aside from increased habitat area, several factors are likely to be involved in Ordovician biomass increase. Increase in the diversity of acritarchs during the Early Middle Ordovician (Tappan & Loeblich, 1973; Martin, 1996; Katz *et al.*, 2004; Servais *et al.*, 2004) may have paralleled an increase in rates of primary production (*P*). As discussed in the previous example, however, primary productivity is in many ways the most difficult parameter to constrain. At the same time, dramatic diversifications occurred in both benthic (brachiopods, bivalves, archaeogastropods, echinoderms, sponges, bryozoa, corals) and planktonic (graptolites, radiolaria) filter and suspension feeding taxa (Vecoli *et al.*, 2005; Harper, in press). The diversification of secondary consumers in several clades also implies a lengthening of food webs and hence increase in consumption efficiency (*c*) and increase in average residence time (*k*) of carbon in the animal biomass pool. Due to its effect on growth efficiency, global climate change may also affect animal biomass. Although the main pulse of Ordovician biodiversification precedes the evidence for widespread terminal Ordovician glaciation, the precise timing of Late Ordovician cooling is a subject of considerable debate (Brenchley *et al.*, 1994; Pope & Read, 1998; Pope & Steffen, 2003; Herrmann *et al.*, 2004a,b; Saltzman & Young, 2005). Cooling temperatures would have raised growth efficiency, increasing standing animal biomass. It is possible that this is a contributing factor to the body-size trends illustrated in Fig. 2, especially given that many Late Ordovician collections in the dataset come from carbonate sequences interpreted to reflect cool-water conditions (Patzkowsky & Holland, 1993). Available evidence suggests it is unlikely that a single factor explains increased animal abundance through the Ordovician. Instead, as with the Permian–Triassic example, a combination of factors, particularly consumption efficiency (*c*) and average residence time (*k*) are most likely to account for increased animal abundance.

CONCLUSIONS

In the case of the Late Permian through Middle Triassic interval it is likely that a combination of factors led to reduced animal biomass in benthic marine ecosystems. Reduced primary productivity is not the only potential control and, in this case, may not even be the most important one. Reduced growth efficiency (g) and a decrease in the turnover rate constant (k) are nearly certain during the Early Triassic and it is likely that consumption efficiency (c) was also reduced. The low abundance of animal shells in Lower Triassic strata therefore can be interpreted to reflect a combination of factors – factors that can be identified and inferred from the fossil record. During the Ordovician radiation, increased biomass of skeletal benthic invertebrates can be most directly tied to increased consumption efficiency with the advent of diverse filter feeders and increasingly effective deposit feeding. Increases in mean body size across several clades and lengthening food webs are also likely to have decreased the rate of turnover within animal communities. Changes in primary productivity and growth efficiency are more difficult to constrain, although increased diversity of acritarchs could signal an increase in the rate of primary productivity. Is the positive correlation between diversity and abundance inferred for the Permian-Triassic and Ordovician examples representative of the entire Phanerozoic? Are some factors more important than others in controlling total animal biomass in the marine realm? It is too soon to tell. Parallel trends in animal diversity and biomass in the Ordovician and Permian–Triassic suggest strong links between animal diversity and animal biomass in the marine realm through deep time that, if confirmed, may help to explain secular trends in animal diversity and ecology through the Phanerozoic.

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