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Escargots through time: an energetic comparison of marine gastropod assemblages before and after the Mesozoic Marine Revolution

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Abstract.—The modern structure of marine benthic ecosystems was largely established during the Jurassic and Early Cretaceous (200-100 Ma), a transition that has been termed the Mesozoic Marine Revolution (MMR). Although it has been suggested that the MMR marks an increase in the average energy consumption of marine animal ecosystems, this hypothesis has not been evaluated quantitatively. In this study, we integrate body size and abundance data from the fossil record with physiological data from living representatives to estimate mean per capita metabolic rates of tropical to subtropical assemblages of shallow-marine gastropods—a major component of marine ecosystems throughout the Meso-Cenozoic—both before and after the MMR. We find that mean per capita metabolic rate rose by ~150% between the Late Triassic and Late Cretaceous and remained relatively stable thereafter. The most important factor governing the increase in metabolic rate was an increase in mean body size. In principle, this size increase could result from secular changes in sampling and taphonomic biases, but these biases are suggested to yield decreases rather than increases in mean size. Considering that post-MMR gastropod diversity is dominated by predators, the net primary production required to supply the energetic needs of the average individual increased by substantially more than 150%. These data support the hypothesis that benthic energy budgets increased during the MMR, possibly in response to rising primary productivity.

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Introduction

A long-running debate in evolutionary paleoecology concerns whether, and how, the flux of energy through animal ecosystems has changed through time. This issue was discussed most famously by Vermeij (1977, 1987, 1995, 2002, 2004) and Bambach (1993, 1999, 2002), both of whom suggested, contra Van Valen (1976), that the aggregate energy requirements of marine animal ecosystems have increased through the Phanerozoic, especially during the Devonian and the Jurassic–Early Cretaceous. Vermeij (1977) dubbed the latter event the ''Mesozoic Marine Revolution'' (MMR). The MMR emplaced benthic ecosystems of essentially modern structure (Valentine 1973; Vermeij 1977; but see Wagner et al. 2006 for an alternate placement of this transition), and arguably represents one of the most profound reorganizations of marine animal ecosystems since the Ordovician. The argument that the energy budgets of marine ecosystems increased during the MMR rests on assessments of a variety of indirect indicators: increases in the proportional diversity of predators (Bambach 1993, 1999, 2002; Bush et al. 2007), frequency of shell-drilling and shell-breaking predation (Vermeij 1983), the prevalence of motility, burrowing, and anti-predatory shell morphologies (Vermeij 1977; Thayer 1979, 1983; Aberhan et al. 2006; Bush et al. 2007), the intensity of bioerosion and bioencrustation (Bromley 2004; Vermeij 2004), and distributions of body sizes (Bambach 1993). However, the magnitude of change in the energy requirements of pre- and post-MMR marine benthic communities remains entirely unconstrained.

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Here we apply a simple energetic model based on the allometric scaling of energy requirements with body size to quantify changes in the mean per capita metabolic rate of marine gastropods in tropical to subtropical fossil assemblages before and after the MMR. Gastropods are well suited for such an analysis because they are well preserved, taxonomically diverse, abundant, and ecologically important in fossil assemblages throughout the Meso-Cenozoic, and have been extensively studied by biologists and paleobiologists. Furthermore, the ecological, morphological, and taxonomic diversification of this group in the Jurassic and Cretaceous is an important component of the MMR (Vermeij 1977; Sohl 1987; Bambach 1993).

Materials and Methods

We use basic scaling principles and comparisons with extant taxa to estimate mean per capita metabolic rates, and principles of trophic energy transfer to estimate the net primary production required to support these energetic needs, for gastropod assemblages representing three pre-MMR intervals (Early, Middle, and Late Triassic), one interval from the early stages of the MMR (Early Jurassic), and three post-MMR intervals (Late Cretaceous, Eocene, and Neogene). Previous work on marine gastropods has established robust correlations between shell volume and soft-tissue biomass (Powell and Stanton 1985) and between biomass and metabolic rate (Vladimirova 2001), allowing individual metabolic rates to be estimated from fossil remains. To further validate the use of fossil data to approximate living communities, and to evaluate the magnitude of energetic gradients in the modern oceans, we also examine Recent gastropod shell assemblages from a shallow Caribbean bay (Miller 1988; Miller et al. 1992) and from slope to abyssal environments in the northwest Atlantic (McClain 2004, 2005; McClain et al. 2004).

To facilitate comparisons among large numbers of fossil assemblages—comprising thousands of genera—over long time scales, we ask a very basic question: what instantaneous energy flux would have been required to sustain the metabolic activity of all of the individuals in the assemblage? The data required to make first-order estimates can be readily gleaned from fossil assemblages, facilitating comparison of large numbers of assemblages within and among time intervals without requiring detailed knowledge of food web structure, growth rates, fecundity, etc., that is difficult to obtain for extinct taxa. We do not attempt to calculate growth efficiency as a function of size or trophic levels, to estimate energy flow patterns among the taxa in an assemblage, or to evaluate other energy expenditures, such as somatic tissue growth and reproduction. Such additional model specificity requires life-history data that are not available for many of the extinct taxa in our data set (for an example using largely extant genera see Powell and Stanton 1985). Respiration is an adequate first-order proxy for overall energy use because it accounts for 30–80% of lifetime energy expenditures in wild populations of extant gastropods (Paine 1971; Huebner and Edwards 1981; Barkai and Griffiths 1988; Morton and Chan 1999).

Selection of Assemblages.—To reduce environmental variation, our analysis is limited to assemblages from paleolatitudes of <40°. The vast majority of assemblages fall within 30° of the equator, except during the exceptionally warm Late Cretaceous–Eocene interval. Assemblages from depositional environments representing likely depths >100 m were excluded. We made exceptions for assemblages, such as the Late Triassic St. Cassian Formation and the Neogene Bowden Formation, which were transported from shallower environments prior to burial. Assemblages from depositional environments representing dysoxic or anoxic conditions, such as the well-described faunas of the upper Pliensbachian (Early Jurassic) of Germany (Nützel and Kiessling 1997; Schubert et al. 2008), were also excluded because they are commonly considered to be dwarfed.

For each time interval, we downloaded all gastropod assemblages from the Paleobiology Database (http://paleodb.org/) that met our latitudinal and environmental criteria and included at least four species and 40 individuals that could be linked to size data. We also included additional Triassic and

Early Jurassic assemblages reported in a variety of published sources and Neogene assemblages from the Panama Paleontology Project database (Collins 2005; http://www.fiu.edu/~collinsl/pppabout.html). We used Recent slope to abyssal gastropod assemblages collected as part of the Bermuda-Gay Head transect (Sanders 1968) that have been described in several publications (Rex et al. 1999; McClain 2004, 2005). Our Recent shallow-shelf data set includes surficial death assemblage collections from a shallow bay in St. Croix, U.S.V.I. (Miller 1988; Miller et al. 1992) and live census data from Florida Bay (Frankovitch 2003). In total, 432 collections were included (394 fossil, 38 living or subfossil; see Appendix 1 online at http://dx.doi.org/10.1666/09066.s1), with a median species richness of 24 and a median sample size of 164 individuals.

Estimating Metabolic Rates.—Our approach to estimating metabolic rates is similar to that applied by Finnegan and Droser (2008) to Ordovician trilobite and brachiopod assemblages. Following Gillooly et al. (2001), we estimated the basal metabolic rate (B_{ind}) of an individual of body mass M as

$$B_{\text{ind}} = B_0 e^{-E/kT} M^{3/4} \qquad (1)$$

where E is the average activation energy of rate limiting biochemical metabolic reactions (on average ~0.65 eV), k is Boltzmann's constant, T is the absolute temperature (°K) at which biochemical reactions take place (equal to the ambient environmental temperature for ectotherms such as gastropods), and B_0 is the standard metabolic rate, a coefficient representing the average mass- and temperature-compensated basal metabolic rate (in Watts/g) of the higher taxon to which the individual belongs. B_0 values are typically estimated at the class or ordinal level (we discuss the derivation of M, B_0, and T estimates below). Holding T constant for all individuals in an assemblage, the mean per capita metabolic rate (B_{avg}) of an assemblage of N individuals is

$$B_{\text{avg}} = \frac{e^{E/kT} \sum_{i=1}^{N} B_{0i} M_i^{3/4}}{N} \qquad (2)$$

where B_{0i} and M_i are the mass- and temperature-compensated basal metabolic rate of the taxon to which the ith individual belongs and the body mass of the ith individual, respectively. This model has been criticized (Kozlowski and Gawelczyk 2002), but substituting a more traditional Q_{10} formulation for temperature dependence of metabolic rate has very little effect on our calculated trends in B_{avg}. The prevalence of 3/4 scaling across taxa is debated (Dodds et al. 2001), but this coefficient has been shown to fit gastropods quite well (Vladimirova 2001). As long as the coefficient is assumed to have been constant through time, substituting any value between 2/3 and 1.0 has only a minor effect on the magnitude of observed trends.

Abundance.—Abundance was tabulated by counting of the number of individuals assigned to each genus in each assemblage. Subfossil molluscan assemblages have been shown to record an accurate signal of rank-order abundance (Kidwell 2001); the degree to which numerical abundance is accurately preserved remains an open question. However, using rank-abundance rather than numerical abundance to weight genus occurrences does not significantly alter the observed pattern.

Body Size Distributions.—We based our body size estimates on a database of the maximum volumes (M_{max}) of figured specimens in taxonomic monographs, which have been shown to capture marine invertebrate size trends with variable but generally high accuracy (Kosnik et al. 2006; Krause et al. 2007). This database, available upon request, currently includes maximum size estimates for more than 4000 species representing more than 1000 genera in the early Mesozoic and Late Cretaceous–Neogene. Our M_{max} estimates are based on a conical approximation of shell shape, which has been shown to capture most of the variation in soft tissue mass among extant marine gastropods (Powell and Stanton 1985). Triassic–Early Jurassic size data are from the database compiled and described by Payne (2005), since extended through the Late Triassic and Early Jurassic. Most Late Cretaceous (Campanian–Maastrichtian) and Eocene size data are those previously discussed by Kosnik (2005). Neogene size data come from a variety of sources, but draw heavily from the comparatively well described faunas of the Caribbean Basin (Woodring 1928, 1957–1982; Weisbord 1962; Jung 1965, 1969; Collins and Coates 1999; Todd et al. 2006). MALACOLOG (Rosenberg 2009) was used as a primary source to compile size data for Recent shallow-shelf assemblages.

Many paleoecological publications identify the individuals in fossil assemblages only to the genus level. In order to include these collections in our analysis, we assigned body size at the genus level (subgenera elevated to genus status) rather than the species level. We assigned each genus occurrence a maximum body size based on the geometric mean of $M_{\max}$ for all species in our database within the matching genus and time interval. Genus size estimates are based only on species extant within each time interval, and hence are independent between time intervals. Using species rather than genus as the basis for size estimates substantially reduces the number of assemblages that can be analyzed, but does not significantly alter observed B_{avg} trends (results not presented). We included only assemblages for which >80% of the taxa and >80% of the individuals could be matched to a genus-level size estimate. Using more restrictive criteria of 90% or 100% matching to body size data reduces the size of the data set but does not otherwise alter the results significantly.

To confirm that fossil data accurately capture size differences among genera, we compared the geometric mean of maximum fossil size of species in 216 genera or subgenera that are both represented in our Neogene fossil size database and have corresponding values for living species in MALACOLOG (Rosenberg 2009), a database of extant species. These two data sets are strongly correlated, indicating that there is little systematic difference in mean size between extant and extinct members of a genus (Fig. 1).

Ideally, the sizes of all individuals in an assemblage would be measured individually. In practice, however, such data are rarely available because such work is prohibitively time-consuming in large collections. Therefore, we used a database of size-frequency distributions of individuals (minimum $n = 10$, maximum $n = 1168$) in local populations of 49 extant species to parameterize a model of the relationship between the maximum observed size of a species and its population-level size-frequency distribution.

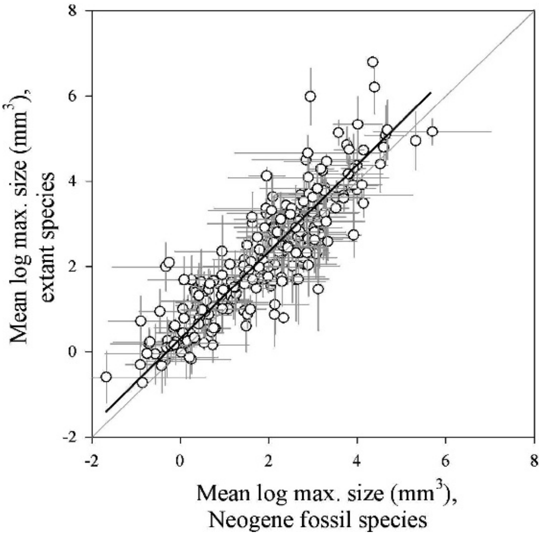

FIGURE 1. The $\log_{10}$ of the geometric average of $M_{\max}$ for species in 216 extant genera plotted against the $\log_{10}$ of the geometric average of $M_{\max}$ for Neogene fossil species in the same genus (supporting reference 16). 1 SD error bars are shown where more than one species is represented, and the line represents unity. The two data sets are strongly correlated ($R = 0.86$, $p \ll 0.001$) with a slope indistinguishable from unity (RMA regression slope = 1.02 ± 0.03, intercept = 0.29 ± 0.09). Mean $M_{\max}$ is lower on average for fossil species than for extant species (by a factor of about 2), but the fossil data accurately record true differences in size among genera. Heavy line indicates RMA regression line, lighter line indicates unity.

Among these extant species, there is a strong linear correlation between $\log_{10}$ maximum size and the mean $\log_{10}$ size of individuals in a population (Fig. 2A); maximum size is a robust predictor of mean size. The shapes of marine gastropod size-frequency distributions are variable in time and space, but most are approximately normally distributed in log space. The $\log_{10}$ size dispersion of individuals in local populations (as measured by the standard deviation of $\log_{10}$ size) is highly variable, but is independent of $\log_{10}$ mean size (Fig. 2B), with a y-intercept of 0.36. That is, species with larger maximum sizes do not exhibit a greater $\log_{10}$ size range at the population level despite the fact that they likely have greater ontogenetic size ranges than smaller species.

Hence, the $\log_{10}$ size-frequency distribution of a population can be modeled as a normal (Gaussian) distribution with probability density function:

$$p(log_{10}x) = \frac{1}{0.36\sqrt{2\pi}} \times exp\left(- \frac{(log_{10}x - (0.95log_{10}Max - 0.59))^2}{2(0.36)^2} \right) \qquad (3)$$

where x is a given body size and *Max* is the maximum observed size of the species. Mean $\log_{10}$ sizes of individuals in modeled populations generated from these parameters are strongly linearly correlated with actual observed mean $\log_{10}$ sizes with a slope indistinguishable from 1 (Fig. 2C), demonstrating that the distortions introduced by the model assumptions are very small. To test whether these assumptions can be reliably applied to fossil assemblages and to taxa not used to parameterize the model, we also plot the modeled versus observed mean $\log_{10}$ sizes of nine species (minimum $n = 10$, maximum $n = 33$) in a size-censused assemblage from

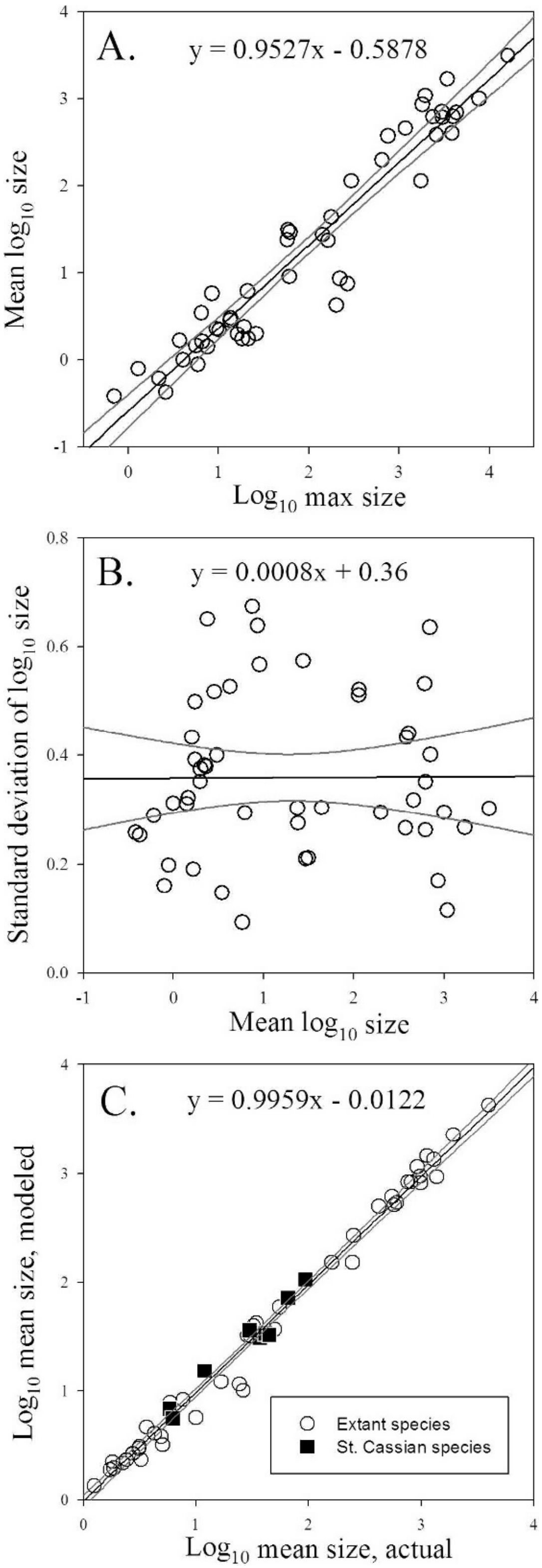

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FIGURE 2. A, Comparison of the mean $\log_{10}$ size and the maximum $\log_{10}$ size of 49 extant gastropod species for which the sizes of all individuals in a population were measured. There is a strong linear correlation in log-log space between mean and maximum size ($R^2 = 0.92$, $p \ll 0.001$). B, Mean $\log_{10}$ size versus the standard deviation of $\log_{10}$ size for the same data set. There is no correlation between the two, indicating that the size dispersion of individuals in the population is unrelated to mean size. C, Comparison of $\log_{10}$ mean size for actual populations of the species in A and B and $\log_{10}$ mean size of individuals in modeled log-normal populations. Modeled populations are based only on the maximum observed size of the species, with the mean of the log-normal distribution calculated based on the regression in A and a fixed standard deviation of 0.36 based on B. Open circles are the extant species used to parameterize the model; black squares are nine species from a size-censused assemblage from the Upper Triassic St. Cassian Formation, which were not included in the parameterizations in A and B. The extremely strong correlation between real and modeled $\log_{10}$ mean sizes for both extant species and fossil species ($R^2 = 0.99$, $p \ll 0.001$) suggests that the noise introduced by the model assumptions is small relative to true $\log_{10}$ mean size differences among species.

the Upper Triassic St. Cassian Formation (Nützel et al. 2010). The size-frequency model predicts the mean $\log_{10}$ size of these species with high accuracy (Fig. 2C).

Whole-assemblage size-frequency distributions were generated by drawing the number of individuals reported for each genus from distributions modeled as described above. We compared the whole-assemblage size-frequency distributions generated in this manner to three assemblages (two extant and one fossil) for which sizes of all individuals in the assemblages were measured (Fig. 3). Although the actual and modeled distributions differ in detail, with the modeled distributions tending to be smoother and less peaked (lower kurtosis), these differences are minor compared to the differences among assemblages, which are well reproduced by the model. Once modeled in this manner, individual size estimates were converted to soft-tissue mass (M) estimates using the empirical relationship between biovolume and biomass demonstrated by Powell and Stanton (Powell and Stanton 1985).

Standard Metabolic Rates.—To assign B_0 values to living and extinct genera, we use the average B_0 of $9.91*10^7$ W/g$^{3/4}$ given for multicellular ectotherms by Gillooly et al. (2001) as a baseline value, and multiply this by the ordinal-level average coefficients (''*a*'' coefficients, which are mathematically equivalent to B_0) reported by Vladimirova (2001). The latter source uses outdated higher taxonomic terminology (e.g., ''Mesogastropoda''), and hence we reclassified all taxa in our database according to this scheme. Family-level B_0 measurements were used where available; otherwise, average B_0 values were assigned at the ordinal level. Genera that could not be confidently assigned to an order were assigned the average B_0 for other genera in that time interval; unassigned genera never account for more than 8% of occurrences in any time interval.

There is considerable uncertainty surrounding the systematic relationships of gastropods (Ponder and Lindberg 2005), and, except for the Neogastropoda, the outdated taxonomic orders for which Vladimirova (2001) reports *a* coefficients are known to be polyphyletic (Ponder and Lindberg 2005). Hence, basal metabolic rate estimates cannot be viewed in a phylogenetic context but should instead be considered as averages for general morphological grades. The confidence with which these coefficients can be used to estimate B_0 values thus depends on the degree to which these morphological grades correlate with basal metabolic rate. B_0 assignments are necessarily speculative for groups that have no close living relatives and are of uncertain systematic affinities (e.g., Bellerophontidae, here placed within the Archaeogastropoda). However, such uncertainties cannot substantially distort B_{avg} estimates unless these extinct groups had basal metabolic rates well outside the observed modern range.

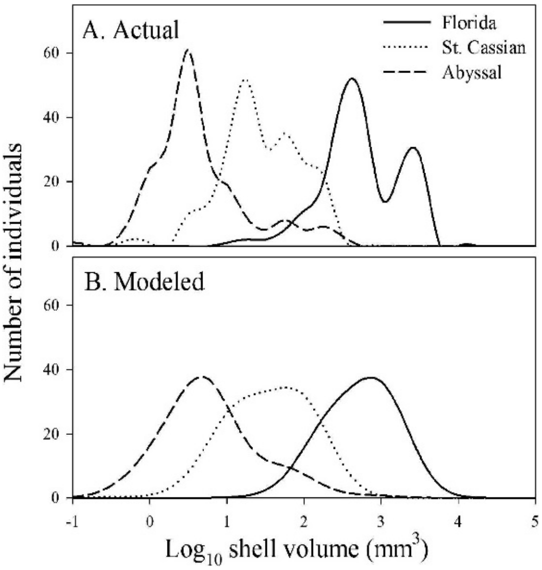

FIGURE 3. Comparison of actual (A) and modeled (B) aggregate size-frequency distributions for one fossil and two living gastropod assemblages. Florida: living individuals in Plot 1, Rabbit Key Basin, Florida (Frankovitch 2003). St. Cassian: fossils from a bed in the Upper Triassic St. Cassian Formation, northern Italy (Nützel et al. 2010). Abyssal: living individuals from station 95 of the deep-sea Bermuda–Gay Head transect, northwest Atlantic (Rex et al. 1999; McClain 2004). Differences between actual and modeled assemblages are minor compared to the differences among these assemblages. Bandwidth and kernelling method held constant for all smoothing lines.

Vladimirova (2001) reports *a* coefficients for tropical and subtropical representatives of the Neogastropoda and ''Mesogastropoda'' that are somewhat higher than the global average, and somewhat below-average *a* coefficients for tropical and subtropical members of the ''Archaeogastropoda.'' Given that our data are limited to the Tropics and subtropics it may be more appropriate to use these coefficients for our estimates; doing so would increase the mean B_0 differences between the pre- and post-MMR assemblages. However, the tropical and subtropical a coefficients reported by Vladimirova are based on relatively few measurements (65, versus 158 in the global average), and hence we used the global averages to provide a more conservative estimate.

Trophic-Level Assignments.—The vast majority of pre-MMR genera, and many post-MMR genera, are extinct. Hence, trophic assignments were for the most part done at the family level or higher. Virtually all extant neogastropods are carnivores (predators, scavengers, parasites, or browsers on colonial invertebrates) (Hughes 1986; Vermeij 1987; Beesley et al. 1998) and this appears to be the case for most extinct representatives of the group as well (Vermeij 1977; Sohl 1987). Because extant neogastropods consume a wide variety of prey items, from colonial invertebrates to polychaetes, clams, and fish (Hughes 1986), it is difficult to assign extinct genera to a precise trophic level with confidence. We therefore make the simplifying assumption that all carnivorous taxa were primary carnivores. The great majority of extant taxa formerly assigned to the ''Archaeogastropoda,'' in contrast, are primary consumers of one kind or another: suspension feeders, herbivorous grazers, or detritivores (Hughes 1986; Vermeij 1987; Beesley et al. 1998); a few extinct Paleozoic groups, such as the Platyceratidae, may have been ectoparasites (Gahn and Baumiller 2003; Gahn et al. 2003; but see Sutton et al. 2006). The ''Mesogastropoda'' include predators such as the Naticidae and carnivorous browsers and parasites such as the Architectonicidae, Mathildidae, and Triphoridae, as well as many primary consumers. We used the NMITA gastropod diets database (Todd 2000, http://porites.geology.uiowa.edu/database/mollusc/Gastropod_diet.html), to assign ''mesogastropod'' families to trophic groups. We assigned Triassic and Early Jurassic ''naticids'' as carnivores, following Fürsich and Jablonski (1984). In fact, these genera were probably neither carnivorous nor true naticids (Bandel 1999; Kase and Ishikawa 2003), but this assignment is conservative in that it tends to reduce rather than inflate estimated energetic differences between pre- and post-MMR assemblages.

Temperature.—Because direct paleotemperature proxy data (e.g., $\delta^{18}O$) are not available for most assemblages, we assume a temperature of 25°C for the shallow-shelf assemblages. This is the average temperature for the upper 50 m of the water column between 30°N and 30°S latitude in the modern global oceans, based on water column temperature data downloaded from the National Oceanographic Data Center World Ocean Atlas 2005 website (http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html) on 17 October 2008. Although a few assemblages come from deeper water, the great majority of assemblages come from inferred depths of less than 50 m and latitudes lower than 30°. Most assemblages from higher latitudes come from the relatively warm, shallow depositional environments represented by the Late Cretaceous–Eocene U.S. Gulf Coastal Plain sediments, and hence represent warmer temperatures than would otherwise be expected at latitudes higher than 30°. An average temperature of 4°C for the Recent abyssal assemblages is known from direct measurements. To estimate the potential effects of temperature variation through time, we also averaged the mean global temperature estimate of the GEOCARB III model (Berner and Kothavala 2001) over each time interval. Aside from the inherent uncertainty in deep-time historical climate models, the amplitude of globally averaged temperature changes through time is almost certainly much greater than that of the Tropics, which are comparatively buffered (MARGO project members 2009).

Results

Size-frequency distributions for individual assemblages show considerable variation within each time interval, but a clear trend emerges when they are compared across the

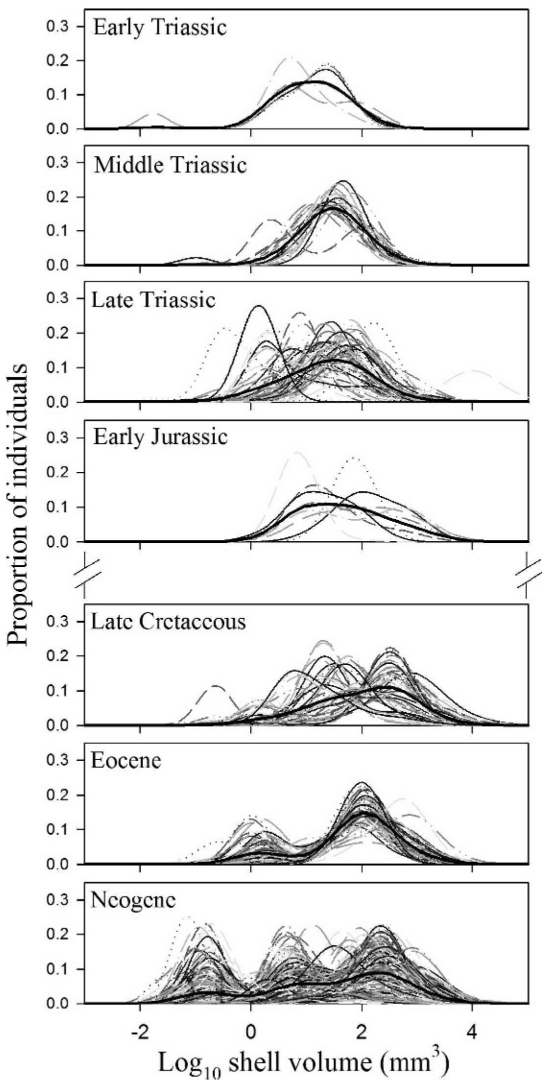

FIGURE 4. Aggregate relative size-frequency distributions, based on the model relating maximum size to individual size-frequency distribution, for all assemblages in each time interval. Shaded gray lines indicate individual assemblages (bandwidth and kernelling method held constant for all assemblages) and heavy black lines are loess regressions (bandwidth = 0.30) through all assemblages to indicate general tendencies of size-frequency distributions through time.

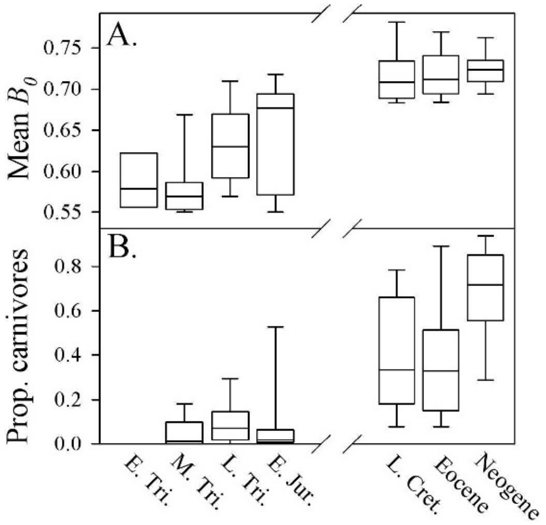

FIGURE 5. A, Distributions of average individual mass- and temperature-compensated basal metabolic rate (B_0). B, Proportions of carnivorous individuals for all time intervals. Horizontal bars represent median values, boxes enclose the 25th through 75th percentiles, and whiskers indicate the 2.5th and 97.5th percentiles.

study interval (Fig. 4). The modal size of individuals in assemblages increases between the Early and Middle Triassic, a pattern that has been previously documented (Fraiser and Bottjer 2004; Payne 2005) and is essentially unchanged from the Middle Triassic to the Late Triassic. Assemblages from the Early Jurassic, an interval preceding the evolution of the carnivorous Neogastropoda (Sohl 1987), but characterized by the early stages of benthic ecological restructuring (Aberhan et al. 2006), appear to be intermediate between the Triassic and the Late Cretaceous. These assemblages show a mode similar to most assemblages in preceding time intervals but a thicker tail of large individuals, though the small number of samples in this time interval and their limited geographic distribution (6, most from Morocco) caution against overinterpretation. The shapes of modeled size-frequency distributions from the Late Cretaceous to the Neogene are variable, but many are left-skewed (greater representation of large individuals) and most have modal sizes considerably larger than any of the Triassic assemblages. The mean size difference between pre-MMR (Middle–Late Triassic) and post-MMR (Late Cretaceous–Neogene) assemblages is substantial (a factor of 2.9) and is highly significant (Mann-Whitney (M-W) $p \ll 0.001$, Kolmogorov-Smirnov (K-S) $p \ll 0.001$).

Pre-MMR (Triassic) and post-MMR (Late Cretaceous–Neogene) assemblages also differ significantly in mean B_0 (Fig. 5A; M-W $p \ll 0.001$, K-S $p \ll 0.001$), reflecting the dominance of most post-MMR assemblages by

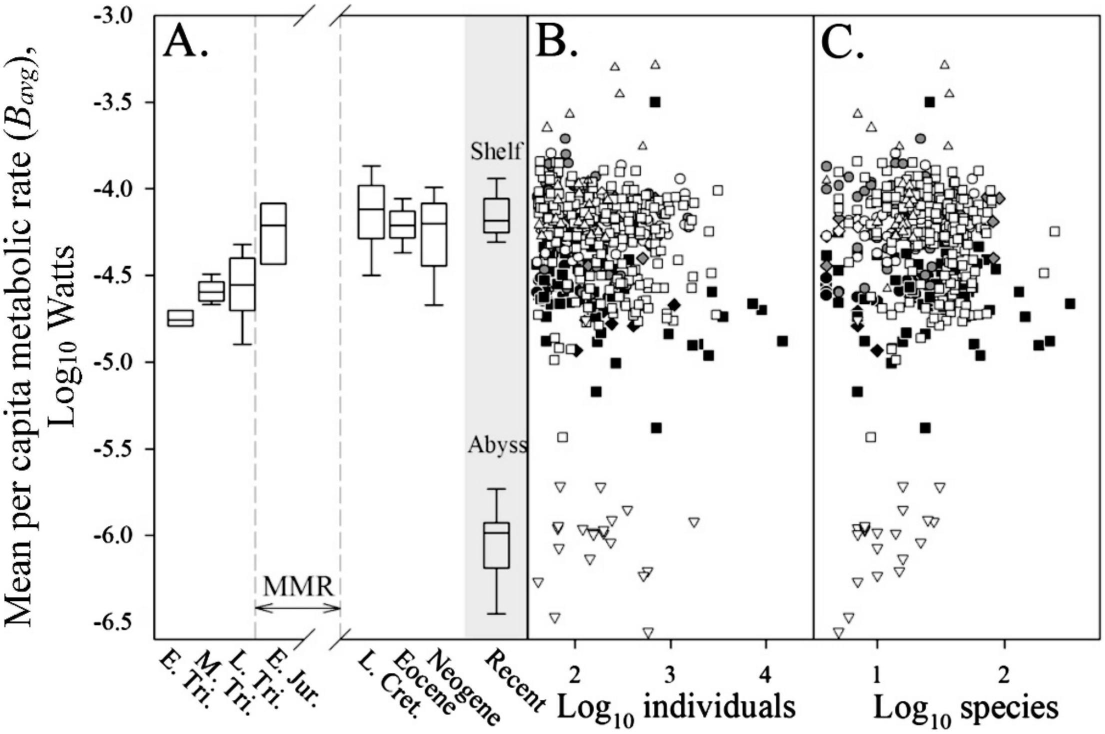

FIGURE 6. A, Boxplots show the distribution of $\log_{10}$ mean individual metabolic rate (B_{avg}) for all assemblages in each time interval. Bars, boxes, and whiskers as in Figure 5. Double-ended arrow marked "MMR" indicates the interval over which the Mesozoic Marine Revolution occurred; break indicates a sampling gap of ~75 Myr between the Early Jurassic and the Late Cretaceous. B, C, B_{avg} plotted against $\log_{10}$ of the total number of individuals (B) and species (C) in each assemblage. Black circles = Early Triassic ($n = 6$); black diamonds = Middle Triassic ($n = 16$); black squares = Late Triassic ($n = 58$); gray circles = Early Jurassic ($n = 9$); gray diamonds = Late Cretaceous ($n = 56$); white circles = Eocene ($n = 64$); white diamonds = Neogene ($n = 175$), white triangles = Recent shallow subtidal ($n = 17$); white inverted triangles = Recent slope-abyssal ($n = 20$).

neogastropods and "mesogastropods." Both of these groups have higher basal metabolic rates on average than the less derived groups that dominate pre-MMR assemblages (Vladimirova 2001), perhaps reflecting the high respiratory quotients associated with digestion of animal tissue (Sterner and Elser 2002). This transition is also reflected in proportions of carnivorous individuals (Fig. 5B; M-W $p \ll 0.001$, K-S $p \ll 0.001$; see additional discussion below), as has been previously discussed by other workers (Vermeij 1977, 1987; Sohl 1987; Bambach 1993, 2002; Bush et al. 2007).

Driven by these trends, mean per capita metabolic rate (B_{avg}) estimates show a substantial increase from the Triassic to the Neogene, and the mean B_{avg} of pre- and post-MMR intervals differs significantly (Fig. 6A; M-W $p \ll 0.001$, K-S $p \ll 0.001$). Mean B_{avg} rises from the Early Triassic to the Middle Triassic, and then rises again between the Late Triassic and the Early Jurassic. Early Jurassic samples already show a B_{avg} range similar to the Late Cretaceous–Neogene range, although once again the small number of Early Jurassic samples warrants caution. As predicted by the hypothesis that the MMR represents a unique and stepwise increase in ecosystem energy budgets, there is little change in B_{avg} from the Late Cretaceous to the Neogene, despite explosive global diversification of marine gastropods, especially neogastropods, over the same interval (Bambach 2002; Sepkoski 2002). Importantly, although sample size varies over three orders of magnitude among the assemblages in our data set, the differences in B_{avg} distribution between pre- and post-MMR assemblages do not generally show a strong dependence on sample size (Fig. 6B) or species richness (Fig. 6C).

Late Cretaceous–Neogene B_{avg} estimates are generally similar to B_{avg} estimates derived from a census of subfossil skeletal remains in a shallow Caribbean bay (Fig. 4A) by Miller and colleagues (Miller 1988; Miller et al. 1992). The fact that these assemblages have been found to be generally comparable to co-occurring live communities with respect to relative abundance structure (Miller 1988; Miller et al. 1992; Kidwell 2001) implies that the general B_{avg} range observed in the Late Cretaceous–Neogene is biologically reasonable, and that the unavoidable overprint of taphonomy and time-averaging may not be severe (see ''Discussion'').

For comparison with the fossil and Recent subfossil assemblages from shallow subtidal environments, we also calculated B_{avg} for food-limited modern deep-sea (slope to abyssal) gastropod assemblages from the northwest Atlantic (Rex et al. 1999; McClain 2004), which receive only 1–3% of primary production from surface waters (Jahnke 1996). These assemblages show B_{avg} values far below even those of the Early Triassic shallow-shelf assemblages (Fig. 6A), demonstrating that the trend observed in fossil assemblages, while striking, falls well within the range observed along productivity gradients in the modern ocean. The median B_{avg} of shallow-shelf assemblages is almost two orders of magnitude greater than that of deep-sea assemblages, as would be expected if B_{avg} tracks energy availability.

As noted above, most pre-MMR assemblages are strongly numerically dominated by primary consumers, whereas post-MMR assemblages commonly include a large proportion of carnivores (active predators, scavengers, carnivorous grazers, and ectoparasites) (Fig. 5B). Because energy from primary production is transferred inefficiently through primary consumers before being consumed by carnivores, the net primary production (NPP) ultimately required to support a carnivore is far greater than that required to sustain a primary consumer of the same size (Kerr and Dickie 2001; Powell et al. 2001). Transfer efficiencies between successive trophic levels in marine ecosystems average about 0.1 (Kerr and Dickie 2001; Powell et al. 2001), so that the NPP required to support a primary carnivore is ten times that required to support a primary consumer. To account for their greater energetic footprint, we multiplied B_{ind} estimates by 10 for all carnivorous individuals and then recalculated mean per capita energy consumption for all assemblages to estimate the primary energy required to sustain them directly or indirectly. Using a coefficient of 10 for all carnivores is conservative in that some neogastropods are in fact secondary or even tertiary carnivores, with commensurately greater energetic footprints. When trophic transfer efficiency is thus accounted for, pre- versus post-MMR differences in the amount of energy from primary production required to sustain the average individual are much greater than implied by B_{avg} differences alone: the energetic footprint of the average Late Cretaceous–Recent individual is seven to eight times greater than that of the average Middle to Late Triassic individual (Fig. 7).

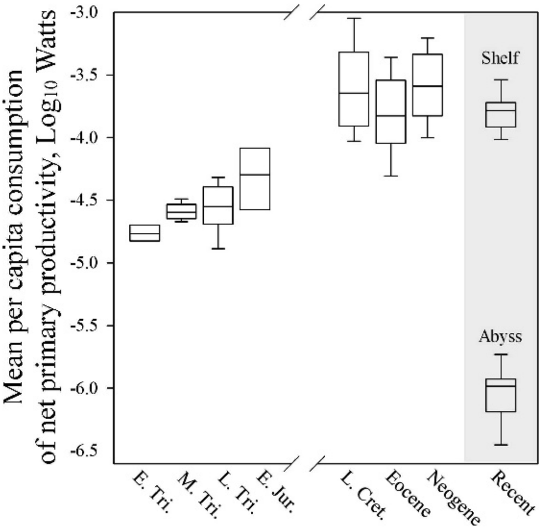

FIGURE 7. Distributions of $\log_{10}$ estimated mean individual NPP consumption for fossil assemblages in each time interval. Bars, boxes, and whiskers as in Figure 5.

This method of estimating total NPP consumption assumes that all energy consumed by gastropod carnivores was derived from other, non-gastropod prey groups. Given that some portion of energy is recycled via gastropod-on-gastropod predation, it will produce somewhat inflated estimates of

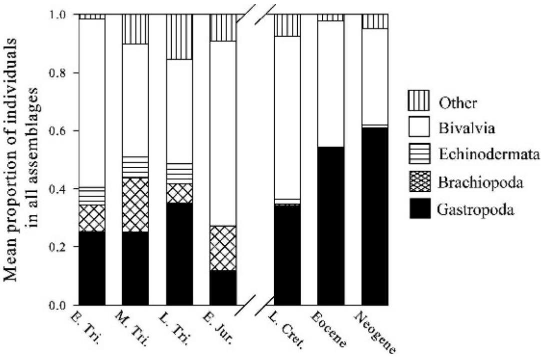

FIGURE 8. The mean relative abundances of major taxonomic groups in shallow to deep-subtidal, low-latitude (<40°) collections included in the Paleobiology Database as of 16 March 2009. Only collections representing at least three classes (to eliminate taxon-specific collections) and including at least 50 individuals are included. Relative abundances were calculated for each collection individually, and were then averaged within each time interval.

NPP consumption. However, carnivore:non-carnivore ratios in gastropod assemblages suggest that the amount of gastropod-on-gastropod predation cannot be large. If all gastropods in a given assemblage fed on other gastropods in the assemblage, the expected carnivore:non-carnivore ratio would be about 1:10, whereas this ratio in fact commonly exceeds 1:2 in post-MMR assemblages (Fig. 5B). Thus, the true change in NPP consumption likely falls somewhere between the minimum, 150% increase estimated on the basis of body size and B_0 alone, and the maximum, order-of-magnitude increase estimated on the assumption that all carnivores consumed non-gastropod prey.

Discussion

Our quantitative estimates of energy consumption suggest that the mean per capita basal metabolic rate of gastropods in shallow-shelf environments rose by a factor of ~1.5 between 200 and 80 Ma. Accounting for the Late Mesozoic–Cenozoic increase in the prevalence of carnivory among gastropods, this implies an increase by as much as a factor of 8 in the per capita consumption, direct or indirect, of energy from primary producers (NPP). In principle, such an increase could have been compensated for by a decrease in population density so that total NPP consumption remained constant. This scenario is clearly not the case, however, as marine invertebrate assemblages in the Paleobiology Database show a substantial increase in the relative abundance of gastropods between the Triassic and the Cenozoic (Fig. 8), largely at the expense of groups such as brachiopods and crinoids, which have comparatively low metabolic rates (Bambach 1993). Additionally, a secular increase in the average thickness of shell beds in shallow-marine deposits suggests that the overall size and/or abundance of skeletonized animals increased through this interval as well (Kidwell and Brenchley 1996). Thus, rather than being offset by compensatory ecological trends, the mid-Mesozoic rise in energy demand within the Gastropoda is likely reflective of a more general pattern: the rise to prominence of the Neogastropoda within the Gastropoda paralleled a shift toward ecological dominance of benthic communities by more metabolically active clades, particularly (but not exclusively) carnivores (Bambach 1993, 2002; Madin et al. 2006).

These results are consistent with the hypothesis that the energy budgets of marine ecosystems rose during the mid-Mesozoic, but the effects of some potential biases should be considered in more detail. First, and most importantly, our analysis treats fossil assemblages as if they were biological communities, despite abundant evidence that time-averaging, taphonomy, and collection biases can skew both the relative abundance structure and the size-frequency distributions of fossil assemblages relative to the communities from which they derive (Cummins et al. 1986; Kidwell and Bosence 1991; Kidwell 2001; Cooper et al. 2006; Kosnik et al. 2007, 2009; Sessa et al. 2009; Hendy 2009). Although these effects complicate comparisons between living communities and fossil assemblages (but see Kidwell 2001, 2002 as well as comparisons below), they are somewhat less problematic when comparing fossil assemblages through time, because all such assemblages have been filtered through similar biases. Our analyses of time-averaged fossil assemblages do not capture seasonal and annual changes in relative abundance structure and size-frequency distributions driven by larval recruitment cycles (Powell et al. 1984; Staff et al. 1986) and short-period turnover in community structure, but this smoothing is advantageous in that it reduces volatility and makes it easier to recognize long-term trends (Kowalewski 1997; Behrensmeyer et al. 2000). Nevertheless, biases that may vary in direction or intensity between the Early Triassic–Early Jurassic and the Late-Cretaceous–Neogene intervals deserve consideration. Below we discuss some of these, specifically environmental heterogeneity, lithification bias, uncertainty in assigning metabolic rates, and temperature variability, before considering the implications of our results for some hypotheses related to the MMR.

Environmental Heterogeneity.—Environmental and/or geographic variation in the composition of gastropod assemblages is one potential source of error. Systemically biased sampling of environmental size gradients through time could, in theory, produce the appearance of a size increase where none in fact occurred. Like many other marine taxa, extant gastropods exhibit depth-related body size gradients (Rex et al. 1999; Roy 2002; Olabarria and Thurston 2003; McClain 2004), and mean body size may increase at high latitudes (Olabarria and Thurston 2003). However, size differences observed over the limited bathymetric and latitudinal range included in our data set are insufficient to account for the magnitude of the mean size increase between pre- and post-MMR assemblages. Similarly, although gastropod size distributions may vary regionally (Vermeij 1978), the observed secular size increase far exceeds the differences observed between different tropical regions in the modern oceans (Vermeij 1978; McClanahan and McClanahan 2002). It is also striking that modeled size-frequency distributions are generally similar in the Middle to Late Triassic and the Late Cretaceous–Neogene despite the fact that the size data used to generate these distributions were collected independently within each time interval.

Nonetheless, size-frequency distributions within each interval do exhibit considerable variation, likely reflecting unrecognized environmental and/or taphonomic gradients. For example, the exceptionally small sizes reported for Early Triassic gastropods (Fraiser and Bottjer 2004; Fraiser et al. 2005; Payne 2005) may be in part a reflection of biased sampling (Brayard et al. 2010; Nützel et al. 2010). Many of the collections in our Late Triassic data set come from the exceptionally preserved mollusk faunas of the St. Cassian Formation of northern Italy (Zardini 1978). The prevalence of small gastropods in this fauna has been noted by many workers (Nützel et al. 2010 and references therein), prompting suggestions that the fauna is dwarfed. Although very large individuals do seem to be absent or rare in the St. Cassian, the small mean size also reflects the comparative ease of extracting very small individuals from this poorly lithified unit (Nützel et al. 2010). Moreover, the modal maximum size among species from the St. Cassian Formation is only slightly smaller than that of Late Triassic species from other units (Fig. 9). Even among the Late Triassic assemblages in our data set that contain larger genera, these genera tend to be relatively rare. Late Triassic assemblages that are dominated by very large genera are

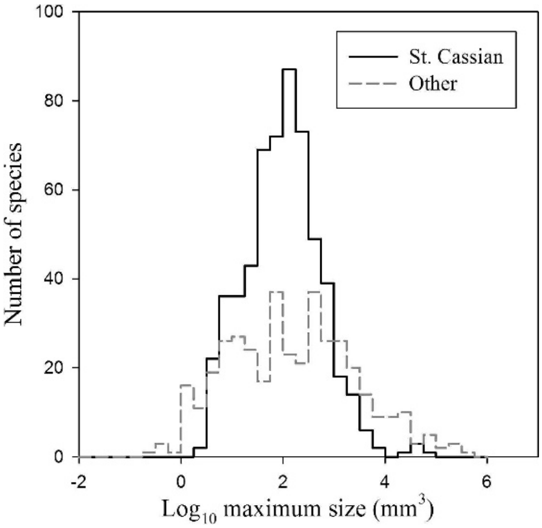

FIGURE 9. Histogram of the maximum $\log_{10}$ body sizes of Late Triassic species from the St. Cassian Formation (Zardini 1978) compared to a histogram of the maximum $\log_{10}$ body sizes of Late Triassic species from other stratigraphic units. Although very large species are almost absent in the St. Cassian, the modal size of St. Cassian species is only slightly smaller than that of Late Triassic species from other units.

known from some regions (Nützel et al. 2010) and also occur in our Late Triassic data set (e.g., sample 95c, from the Hungarian Dachsteinkalk; Appendix 1, online) but these appear to be exceptional.

Lithification Bias.—Lithification often leads to undersampling of small individuals and species, especially microgastropods (species with a maximum dimension <5 mm), presumably because they are more difficult to extract and/or identify (Cooper et al. 2006; Sessa et al. 2009; Hendy 2009). This effect is a particular source of concern because most pre-MMR assemblages are lithified to some degree, whereas many post-MMR assemblages are not. Most gastropod species in the modern oceans are comparatively small (Bouchet et al. 2002) and this has probably been true throughout their history. Hence, it is likely that many or even most species are missing or underrepresented in collections from lithified sediments (Sessa et al. 2009; Hendy 2009). This bias cannot be a major factor in driving the observed pattern, however, because it should lead to greater underrepresentation of small individuals in the early Mesozoic relative to the Late Cretaceous–Cenozoic—the opposite of the bias required to generate the observed pattern of increased per capita energy use. Microgastropods may be underrepresented in some collections from unlithified sediments because the smallest size fraction is commonly discarded prior to study (Kidwell 2001), or ignored entirely during surface collection, but gastropods as small as or smaller than the smallest early Mesozoic genera are well represented in Late Cretaceous–Cenozoic, especially Neogene, assemblages (Fig. 4).

To test for the possibly variable sampling of microgastropods, we reanalyzed the data after removing all taxa with a maximum dimension <5 mm from our data set. This approach increases mean per capita metabolic rate estimates in all data sets by increasing the mean size of individuals, but does not substantially change the timing or magnitude of the observed increase in B_{avg}, and pre- and post-MMR B_{avg} distributions remain significantly different (Fig. 10A; M-W $p \ll 0.001$, K-S $p \ll 0.001$). These differences in energy use also remain if the largest 20% of genera are excluded from each assemblage (Fig. 10B; M-W $p \ll 0.001$, K-S $p \ll 0.001$). Hence the mid-Mesozoic increase in mean body size and B_{avg} reflects a shift in the central tendency of body size distributions within gastropod assemblages rather than changes in the extremes.

Uncertainty in Assigning Metabolic Rates.—The second component of the mid-Mesozoic increase in per capita energy consumption is a rise in the mean basal metabolic rate (B_0) (Fig. 5B), which reflects the differential diversification of the Neogastropoda and "Mesogastropoda." In fact, differences in B_0 coefficients probably understate true differences in energy demand because they do not account for metabolic expenditures associated with activity above the resting state. The predatory and scavenging lifestyles of Neogastropods likely require, on average, more frequent and sustained activity than the grazing and suspension-feeding lifestyles that have been inferred for most early Mesozoic species (Vermeij 1977, 1987, 2004; Bambach 1993, 1999). Hence, accounting for average activity level in addition to basal metabolic rate would increase the differences in B_{avg} between pre- and post-MMR assemblages, perhaps substantially.

The coarse taxonomic level at which B_0 coefficients were assigned and the fact that some of the extant orders for which Vladimirova (2001) reports B_0 coefficients are known to be para- or polyphyletic (Ponder and Lindberg 2005) is a further concern. We evaluated the potential impact of faulty B_0 assignments by ignoring the ordinal-level differences in underlying physiology and instead assigning the average B_0 of 0.71 (Vladimirova 2001) to all genera and recalculating B_{avg} trends. This slightly diminishes the observed increase in per capita metabolic rate, but pre- and post-MMR B_{avg} distributions remain significantly different (Fig. 10C; M-W $p \ll 0.001$, K-S $p \ll 0.001$). This is not surprising because mean B_0 varies by less than a factor of 2 among gastropod orders, whereas gastropod body sizes vary by several orders of magnitude. The range of B_0 for gastropods is quite small relative to that

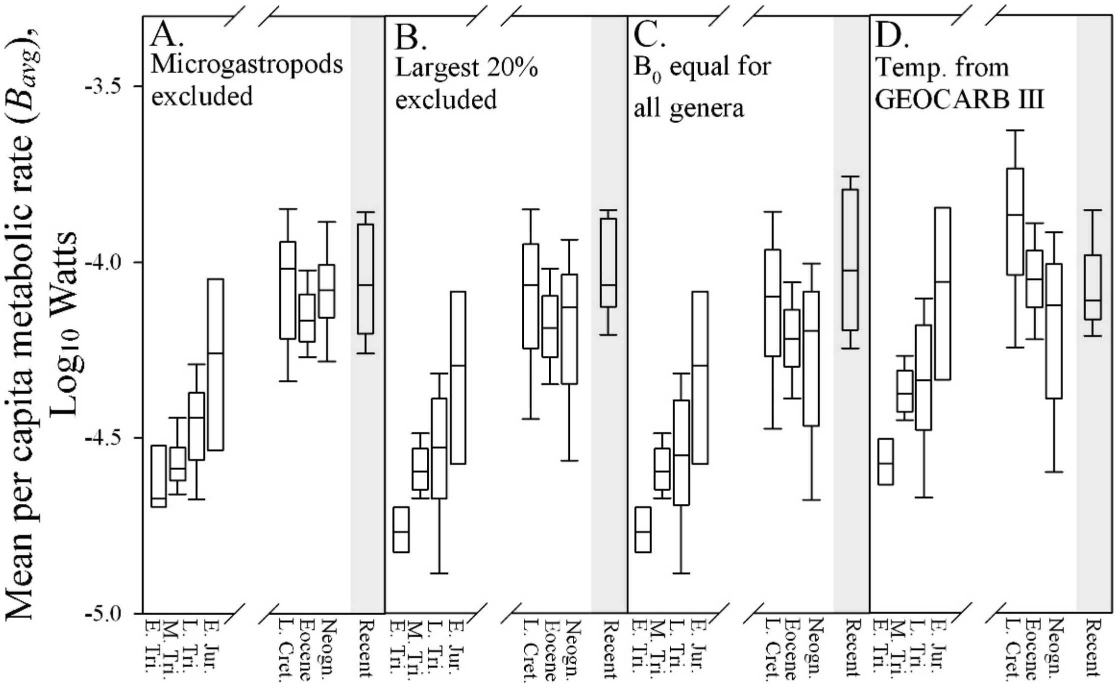

FIGURE 10. Distributions B_{avg} estimates for different manipulations of the data presented in Figure 6. A, Log_{10} B_{avg} distributions after excluding all genera with a maximum dimension of less than 5 mm. B, Log_{10} B_{avg} distributions if the largest 20% of genera in each assemblage are also excluded. C, Log_{10} B_{avg} distributions if all gastropods are assumed to have the same basal metabolic rate (B_0). D, Log_{10} B_{avg} distributions if temperatures are based on the average temperature anomaly predicted for each interval by the GEOCARB III CO_2 model (Berner and Kothavala 2001). Bars, boxes, and whiskers as in Figure 5.

observed among related clades in some other invertebrate groups (Seibel 2007).

Temperature Variability.—Temperature is the last major variable that influences individual metabolic rate after body size, B_0, and trophic level (see eq. 1). Seawater temperatures certainly varied among the assemblages in our data set, but the magnitude of this variation is constrained by our latitude and depth restrictions: the amplitude of tropical temperature variations is generally smaller than that of average global temperature (MARGO project members 2009). Therefore, we assume a constant temperature of 25°C for all shallow-shelf assemblages for our calculations presented in Figure 10A–C. However, even if temperatures are assumed to track modeled atmospheric CO_2 concentrations (Berner and Kothavala 2001), we still observe a significant increase in B_{avg} between the Triassic and the Late Cretaceous (Fig. 10D; M-W $p \ll 0.001$, K-S $p \ll 0.001$). Thus, the conclusion that per capita energy use increased across the MMR holds for any reasonable assumptions about temperature variability among assemblages or climate change through time.

Implications and Future Work.—Our focus in this paper has been on developing a framework for quantitatively evaluating energetic changes and considering the biases that may affect such estimates. Below we briefly consider some implications of our findings, which can be further evaluated by expanding this approach to other taxa and other time intervals.

Known biases and uncertainties do not appear capable of generating the observed rise in mean body size, per capita metabolic rate, and NPP consumption. In fact, the implied increase in NPP, because it largely reflects well-known and uncontroversial changes in trophic ecology, would remain significant and substantial even in the absence of any change in per capita metabolic rate. Our results therefore support the hypothesis that the MMR marks an increase in the energy budgets of marine animal ecosystems—a hypothesis that is also supported by trends in motility (Bambach 2002; Aberhan et al. 2006; Bush and Bambach 2007) bioturbation intensity (Thayer 1979, 1983) and predation intensity (Vermeij 1983; Bambach 2002; Bush and Bambach 2007).

Like earlier stepwise increases in the standing biomass of benthic ecosystems (Payne et al. 2006; Finnegan and Droser 2008; Novack-Gottshall 2008), this trend must represent either an increase in primary productivity or an increase in the efficiency of energy use (Payne and Finnegan 2006). The latter is unlikely because, as has been argued by Vermeij (2004) and Bambach (1993, 1999), the taxa that rose to dominance during the MMR were likely successful in part because they are on average more powerful—but less efficient—than the taxa that dominated Paleozoic and pre-MMR Mesozoic ecosystems.

We therefore favor rising productivity as an explanation for the observed increase in energy use. One mechanism for driving a mid-Mesozoic increase in primary productivity is enhanced nutrient flux from weathering of rocks, either via increasing submarine volcanism (Vermeij 1995) or via increased continental weathering and nutrient recycling following the diversification of terrestrial angiosperms in the Cretaceous (Bambach 1999). Alternatively, increasing bioturbation may have led to greater nutrient availability via a decrease in the burial efficiency of organic carbon and its associated limiting nutrients, especially phosphate (Thayer 1979, 1983; but see Katz et al. 2005). The weathering scenarios posit that marine ecosystems responded passively to an externally forced increase in nutrient availability, whereas the bioturbation hypothesis raises the possibility of a positive ecological feedback: increasing predation led to greater infaunalization, which led to more efficient nutrient recycling, enhanced productivity, and still greater predation pressure (Thayer 1983; Martin 1996).

The timing of the MMR also coincides with the diversification and rise to ecological dominance of the ''red group'' phytoplankton lineages (calcareous nannoplankton, dinoflagellates, and diatoms) that account for most primary production in the modern oceans (Falkowski et al. 2004; Katz et al. 2004; Falkowski and Knoll 2007). This ecological shift among primary producers may be related to a secular trend in the oxidation state of the oceans. Katz et al. (2004) point out that red group lineages require trace metals that are more readily available in well-oxygenated, nutrient-rich coastal water than they are in the oligotrophic open-ocean settings in which the green algal prasinophyte and cyanobacterial groups that dominated production in the Paleozoic and early Mesozoic flourished (Anbar and Knoll 2002). Both calcareous nannoplankton and dinoflagellates appeared in the Late Triassic and underwent major diversifications in the Early Jurassic (Falkowski et al. 2004); the Early Jurassic also marks the last major occurrence of large concentrations of prasinophytes (Katz et al. 2004). In this context, it is notable that our data suggest that the shift to larger mean size that characterizes post-MMR assemblages may have far preceded the diversification of the Neogastropoda (and of terrestrial angiosperms) in the Cretaceous. The small number of Early Jurassic assemblages cautions against drawing any conclusions at this point, however. These assemblages (from Italy and North Africa; see Appendix 1, online), contain many large genera, but their size range contrasts strikingly with the dwarfed gastropod faunas, excluded from this analysis, that occur contemporaneously in the poorly-oxygenated basins of north-central Europe (Nützel and Kiessling 1997; Schubert et al. 2008).

Delineating the environmental and temporal distribution of such size gradients in more detail, and considering their possible relationship to oxygen and/or productivity gradients, should be an important objective for future work. Expanding the temporal coverage of our data set to fill in the Middle Jurassic–Early Cretaceous interval will provide additional tests of the consistency of the observed pattern, and will further constrain the timing of the increase in per capita metabolic rates. Finally, we intend to expand our data set to include other ecologically important skeletonized taxa, in particular bivalves, to evaluate whether the increase in per capita metabolic rate is apparent in multiple taxa. Concordant trends, like those observed in the early Paleozoic (Novack-Gottshall 2008) are predicted by the hypothesis that marine primary production rose substantially during the mid-Mesozoic.

Conclusions

Application of size-based metabolic models to fossil gastropod assemblages indicates that the mean per capita metabolic rate of marine gastropods in tropical to subtropical shallow-shelf assemblages increase by ~150% between the Late Triassic and the Late Cretaceous, consistent with the hypothesis that the Mesozoic Marine Revolution in the structure of marine ecosystems marks an increase in the energy budgets of marine animal ecosystems (Bambach 1993, 1999, 2002; Vermeij 1977, 1983, 1987, 1995, 2002). This rise reflects increases in both mean body size and mean basal metabolic rate. After accounting for differences in trophic level related to the Early Cretaceous diversification of the carnivorous Neogastropoda, we estimate that post-MMR assemblages required as much as eight times as much energy from primary production as pre-MMR assemblages to support themselves. Taphonomic and collection biases cannot explain the observed trend and do not appear to have altered its apparent magnitude substantially. Nevertheless, further studies, especially studies that quantitatively assess individual size-frequency distributions within fossil assemblage, are required to validate our results. Gastropods are only one component of marine ecosystems, but other lines of evidence suggest that the overall productivity and aggregate metabolic demands of marine benthic ecosystems increased during the Mesozoic. Further work expanding this approach to entire fossil assemblages may help to constrain the timing and magnitude of productivity increase, which may in turn help to differentiate among the various hypotheses that have been suggested to explain this ecological restructuring.

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