

Supporting Information

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SI Text

Metabolic Theory of Ecology. The Metabolic Theory of Ecology (MTE) proposes that individual metabolic rate, B (W), is governed largely by the combined effects of body size, M (g), and absolute temperature, T (K) (1) (Eq. S1):

$$B = b_o M^{3/4} e^{-E(1/kT - 1/kT_c)}, \quad [\text{S1}]$$

where $M^{3/4}$ describes the body size dependence, T_c is some fixed arbitrary temperature for standardization, and b_o is a metabolic normalization independent of size and temperature that may be influenced by resource availability in the environment (2). The Boltzmann–Arrhenius relationship, $e^{-E/kT}$, describes the exponential effects of temperature on aerobic metabolism, where k is Boltzmann's constant (8.62×10^{-5} eV K⁻¹), and E is the activation energy describing the exponential effects of temperature on aerobic metabolism in the respiratory complex (~ 0.6 – 0.7 eV) (1). Other biological rate processes, such as growth rate G , are proportional to mass-specific metabolic rate, B/M , and therefore, they decline with increasing body size (3, 4) (Eq. S2):

$$G \propto B/M = b_o M^{-1/4} e^{-E(1/kT - 1/kT_c)}. \quad [\text{S2}]$$

Biological times, including lifespan, are inversely proportional to the mass-specific metabolic rate (3, 4).

MTE yields predictions on biomass and abundance based on the assumption that total population size per unit area, N_{TOT} , is at equilibrium with the supply rate of limiting resources R (Eq. S3),

$$B_{TOT} = N_{TOT} B \propto R, \quad [\text{S3}]$$

where B_{TOT} is the total rate of metabolism by the population (4). Eq. S3 predicts a linear increase in abundance, N_{TOT} , with resource availability, R , if metabolic rate remains constant. Holding R and B_{TOT} constant, Eqs. S1 and S3 can be combined to predict that abundance should increase with resource availability but decline with increasing size ($\propto M^{-3/4}$) and temperature ($\propto e^{E/kT}$) owing to higher per-individual metabolic demands (5, 6) (Eq. S4):

$$N_{TOT} = (B_{TOT}/b_o) M^{-3/4} e^{E/kT} \propto R. \quad [\text{S4}]$$

By contrast, total standing biomass, M_{TOT} , should increase with body size (Eq. S5),

$$M_{TOT} = N_{TOT} M = (b_o/B_{TOT}) M^{1/4} e^{E/kT} \propto R, \quad [\text{S5}]$$

because of declines in the rate of energy expenditure per unit biomass, B/M , using Eq. S2. The work by Damuth (7) first recognized that population size often declines with body size, because $N_{TOT} \propto M^{-3/4}$ for a given amount of energy (the energetic equivalence rule).

The key assumption used to derive the energetic equivalence rule— R is independent of body size—is not upheld for communities where larger-bodied organisms occupy higher trophic levels. In such instances, MTE predicts a slope steeper than $-3/4$ for the abundance-size relationship (S6),

$$N_{TOT} \propto e^{E/kT} M^{\log \alpha / \log \beta - 3/4}, \quad [\text{S6}]$$

given a predator-to-prey body size ratio $\beta > 1$. This steeper decline arises, because only a small fraction, α , of energy is trans-

ferred from one trophic level to the next ($\sim 10\%$); therefore, fewer resources, R , are available for larger organisms at higher trophic levels. For the special case where $\beta \sim 10^4$ and $\alpha \sim 0.1$, Eq. S6 predicts that $N_{TOT} \propto M^{-1}$, consistent with data in pelagic oceanic food webs (8).

The work by Allen et al. (6) proposed a temperature dependence of species richness, S , by first noting that average population size, $\overline{N_{TOT}}$, for a community comprised of J individuals and S species in an area of size A is equal to $\overline{N_{TOT}} = J/AS$; therefore, the average energy flux per species, $\overline{B_{TOT}}$, is equal to (Eq. S7)

$$\overline{B_{TOT}} = B \overline{N_{TOT}} = BJ/AS. \quad [\text{S7}]$$

Rearranging terms in Eq. S6 under the assumption that total community abundance per unit area, J/A , is independent of temperature yields the prediction that species richness will increase exponentially with temperature in the same way as metabolic rate (Eq. S8):

$$S = S_o e^{-E/kT}, \quad [\text{S8}]$$

where $S_o = b_o M^{3/4} J / \overline{AB_{TOT}}$.

Data. Metabolic rate. We compiled 121 estimates of metabolic rate from 94 marine benthic organisms (9–15). For each metabolic rate measurement, we recorded the temperature at which the experiment was conducted, the mass of the individual, and the depth of collection. For many of these measurements, specific geographic information was not provided that would allow us to derive site-specific estimates of particulate organic carbon (POC) flux. As an alternative, we used depth as a proxy for POC (16, 17). Although temperature varies with depth for depths < 600 m, temperature remains relatively constant at greater depths. By specifically accounting for temperature in our analyses, we can assess whether residual variation is correlated with depth, suggesting an independent effect of carbon flux.

Most of the data represent benthic species from soft-bottom deep-sea habitats. Individuals ranged in mass from 0.001 mg to 8.2 kg, depths ranged from 0 to 4,420 m, and temperature ranged from 2 °C to 29 °C. We also included data for species occurring in higher-productivity chemosynthetic systems. Rates of deep-sea organisms were compared with the rates of shallow water benthic animals from the same studies. Shallow water organisms were included in the metabolic, growth rate, and lifespan datasets to assess whether deep-sea systems were similar to shallow water systems with presumed higher productivity. Metabolic rates were converted to watts.

Individual turnover and growth. Rates of individual turnover (1/ lifespan) include field estimates for 47 species of deep-dwelling vertebrates and invertebrates, field estimates for 175 shallow water fish species (18), and laboratory estimates for 65 species of shallow water fish and assorted aquatic invertebrate species (19). We also included the data for species occurring in higher-productivity chemosynthetic systems. Growth rates (grams year⁻¹) were taken from the literature for species of vertebrates ($n = 99$) and invertebrates ($n = 11$) (20–26).

Biomass, abundance, and average body size. Field-derived estimates of biomass, M_{TOT} , and abundance, N_{TOT} , for constituents of the benthic community—bacteria, meiofauna, macrofauna, and megafauna—were taken from a previously compiled database

(27), which spans the globe (Fig. 1). Data were restricted to samples where M_{TOT} and N_{TOT} for a specific community constituent (e.g., macrofauna) were both estimated using quantitative sampling gear ($n = 444$). Two outliers identified by the partial regression plots were removed from further analysis; removal did not change the significance or lack thereof for individual factors. Average body size was then estimated as $\bar{M} = M_{TOT}/N_{TOT}$. For both this dataset and the diversity dataset, POC flux to the seafloor was estimated from geographic coordinates using the model in the work by Lutz et al. (28). Bottom

temperature data were derived from the World Ocean Atlas 2009 (29).

Species diversity. All samples were collected by epibenthic sleds, which sample near-surface sediments over an area of 10–100 m² per tow. Samples span the Atlantic Ocean (Fig. 1). Samples were washed on a 420- μ m sieve. Locality data are provided in the works by Allen (30) and Stuart and Rex (31). Species diversity was standardized for individual samples by using the Sanders–Hurlbert expected number of species (32) normalized to sample sizes of 50.

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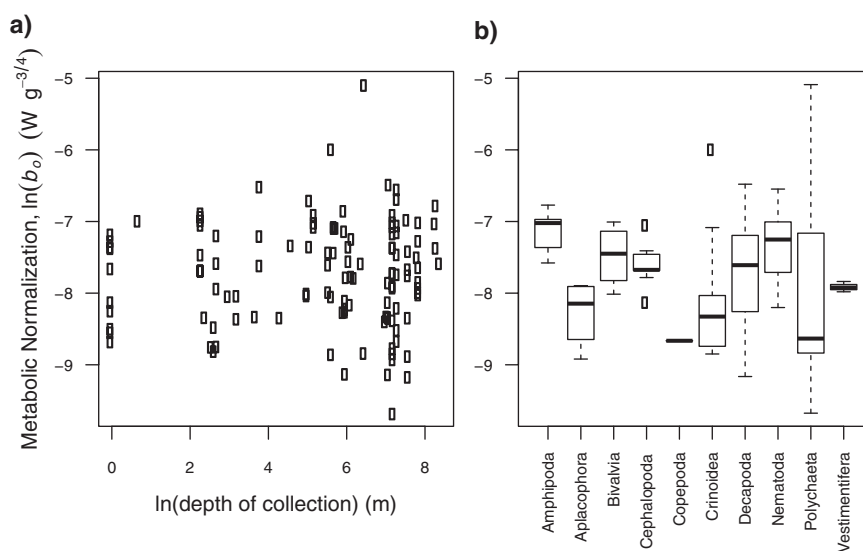


Fig. S1. Variation in the normalization constant of metabolic rates (A) across depth (collection depth in meters), a proxy for carbon flux, and (B) among higher taxa. Normalization constants were calculated using the size–temperature model depicted in Fig. 2.