With frigid temperatures and virtually no in situ productivity, the deep oceans, Earth’s largest ecosystem, are especially energy-deprived systems. Our knowledge of the effects of this energy limitation on all levels of biological organization is very incomplete. Here, we use the Metabolic Theory of Ecology to examine the relative roles of carbon flux and temperature in influencing metabolic rate, growth rate, lifespan, body size, abundance, biomass, and biodiversity for life on the deep seafloor. We show that the relative impacts of thermal and chemical energy change across organizational scales. Results suggest that individual metabolic rates, growth, and turnover proceed as quickly as temperature-influenced biochemical kinetics allow but that chemical energy limits higher-order community structure and function. Understanding deep-sea energetics is a pressing problem because of accelerating climate change and the general lack of environmental regulatory policy for the deep oceans.

Life requires energy. The flux and transformation of energy influences processes and patterns across levels of biological organization. Three distinct types of energy affect biological systems: solar radiation in the form of photons, thermal kinetic energy as indexed by temperature, and chemical potential energy stored in reduced carbon compounds (1). Genomic, phenotypic, and taxonomic diversity and complexity are correlated with variation in energy availability in space and time (1, 2). For example, the acquisition of mitochondria through endosymbiosis allowed for increases in energy expenditure, which in turn, facilitated increases in coding genome size and complexity (3). Global variation in metabolic rates and life history traits, particularly in ectotherms, in part reflects variation in temperature (4). The tremendous range in body size among metazoans is tied both to patterns of carbon accessibility and temperature (5–7). The rapid proliferation of higher-order taxa during the Mesozoic Marine Revolution is posited to have been driven by increases in energy availability (8, 9).

The deep oceans, which encompass depths below 200 m, cover most of Earth and are especially energy-deprived systems. Globally, temperatures of most of the seafloor vary between −1 °C and 4 °C (10). These cold temperatures limit the biochemical kinetics of metabolism. Photosynthetically active radiation is nonexistent, and consequently, primary production is virtually absent, occurring only through alternative pathways, such as chemosynthesis. However, chemosynthesis represents a small percentage of total ocean production (0.02–0.03%) and a small percentage (3%) of carbon flux to nonchemosynthetic systems (11). The chemical energy that sustains most deep-sea organisms is sequestered from sinking particulate organic carbon (POC) derived from primary production in the euphotic zone hundreds of meters to kilometers above. POC flux decreases with depth in the water column, because material is remineralized, and distance seaward from productive coastal regions. At the abyssal seafloor, this downward flux represents less than 1% of surface production (12).

Although the availability of specific types of energy is important at some levels of biological organization in the deep sea, its effects at other levels are unknown. Body size and temperature are primary determinants of metabolic rate for benthic deep-sea organisms (13–15). Previous work indicates that, after accounting for these variables within clades, metabolic rates do not vary with depth (13, 14), which is inversely related to POC flux (16, 17). The influence of energy availability on individual growth rates and lifespan is unknown. At the community level, biomass and abundance generally decline with depth. Direct tests for the influence of POC and temperature on these community attributes are rare, but they suggest only weak effects for temperature (16, 18). Although broad-scale patterns of deep-sea biodiversity are well-established and presumably linked to POC, specific tests of this relationship remain limited (reviewed in ref. 19). In a recent study of species–energy relationships for modern deep-sea mollusks of the North Atlantic, POC had substantially greater predictive power than temperature (20), which is in contrast to findings from fossil assemblages of deep-sea ostracods, where temperature generally prevailed (21, 22). It remains unclear whether these results can be generalized to larger spatial scales and other taxa.

Our meager knowledge of energetics in the deep sea is unfortunate considering the rapid and accelerating climate change and the general lack of environmental policy for conserving deep ecosystems (23). Recent research indicates that global phytoplankton production has declined at a rate of ~1% of the global median per year over the last century (24). Regional-scale changes have been more heterogeneous, with the equatorial Pacific experiencing overall declines of ~50% over the last decade and polar regions experiencing increases of comparable magnitude (25). The deep sea is also warming. The deep Mediterranean water mass has warmed by 0.12 °C since the middle of the last century (26). Deep oceans now store 16–89% more heat (27). These modifications and redistribution of total energy in the oceans will inevitably impact the deep-sea fauna, perhaps rapidly (28–30). Clearly, there is a strong need for a more complete understanding of energetics at the deep-sea floor to enable greater understanding and predictive power for the consequences of forthcoming climate change.

Here, we use the Metabolic Theory of Ecology (MTE) (4) as a framework to understand and link energetics across multiple scales of biological organization in the deep sea. Specifically, we use MTE to examine the relative roles of carbon flux and temperature in influencing metabolic rate, growth rate, lifespan, body size, abundance, biomass, and biodiversity across broad taxonomic and geographic scales (Fig. 1). Specifically, we assess (i) the effects of the availability of thermal kinetic energy (i.e., temperature) and chemical potential energy (i.e., POC) on the deep-sea benthos at different levels of biological organization from individual to community to ecosystem; (ii) the extent that extremely energy-limited systems follow common macroecological patterns; and (iii) how deep-sea ecosystems may be affected by climate change. We show that the relative effects of thermal and chemical energy vary considerably across organizational scales. Consequently, climate change may greatly impact the capacity...
for biodiversity, carbon cycling, and general ecosystem function in the deep oceans.

Results

Metabolic Rate. Body size and temperature account for significant fractions of the variance in metabolic rate for deep-dwelling taxa collected at depths > 200 m (\(R^2 = 0.70; F = 86.11, df = 2, 75; P < 10^{-15}\)) and shallow-dwelling taxa (\(R^2 = 0.44; F = 15.69, \text{degrees of freedom (df) = 2, 40; } \hat{F} < 10^{-5}\)). The two groups exhibit no significant differences with respect to the exponent characterizing size dependence (\(F = 0.38, df = 2, 116; P = 0.69\)), the activation energy characterizing temperature dependence (\(F = 1.16, df = 2, 116; P = 0.32\)), or the metabolic normalization characterizing the size- and temperature-corrected rates (\(F = 0.13, df = 1, 117; P = 0.72\)). Thus, shallow- and deep-dwelling benthic organisms are well-characterized by a single metabolic rate model (solid lines in Fig. 2A and B), with a mass exponent (−0.20) that is close to but slightly lower than the MTE-predicted value of −0.25 (95% confidence interval (CI) = −0.23 to −0.17), and an activation energy (0.47 eV) that includes the predicted range of 0.6–0.7 eV (95% CI = 0.32–0.62 eV) (Eq. S2).

After accounting for size and temperature using these parameter estimates, metabolic rate does not vary significantly with depth (\(F = 0.04, df = 1, 119; P = 0.84\)) (Fig. S1), which serves as a proxy for carbon flux to benthic organisms, but it does vary significantly among taxonomic groups (\(F = 2.14, df = 9, 111, P = 0.03\)) (Fig. S1). Hydrothermal vent and methane seep taxa generally seem to have metabolic rates near other deep-sea taxa and shallow sea taxa when mass and temperature are accounted; the exception is Methanoarcula dendrobranchiata, which seems to have a higher than expected metabolic rate.

Individual Turnover and Growth. For the combined dataset, organisms that are smaller and living at warmer temperatures exhibit higher rates of individual turnover (\(R^2 = 0.91; F = 1424, df = 2, 291; P < 10^{-15}\)). The 95% CIs for the coefficients encompass MTE-predicted values of −0.25 for the mass exponent (−0.25; 95% CI: −0.26 to −0.24) and the predicted range of 0.6–0.7 eV for the activation energy (0.56 eV; 95% CI: 0.49–0.62 eV) (Eq. S2). Significant differences in turnover rate exist between data sources: size and temperature both have significant independent effects on longevity, and together, they account for the majority of the variance for laboratory-cultured organisms (both \(P < 10^{-15}\); \(R^2 = 0.99\)), shallow-dwelling fish (both \(P < 10^{-15}\); \(R^2 = 0.60\)), and deeper-dwelling rockfish (mass: \(P < 10^{-10}\); temperature: \(P = 0.01; R^2 = 0.67\)). However, for deep-sea invertebrates, only mass is significant (mass: \(P = 0.005\); temperature: \(P = 0.78; R^2 = 0.50\)), despite the wide temperature range (2.5 °C to 17 °C). The exponent characterizing the size dependence does not differ significantly among the four data sources (\(F = 1.92, df = 3, 285; P = 0.13\)), and the activation energy does not differ significantly among the three datasets exhibiting significant temperature effects (\(F = 2.18, df = 2, 285; P = 0.12\)). Thus, all four datasets are well-characterized by a single mass exponent (−0.24) that is consistent with the MTE-predicted value of −0.25 (95% CI: −0.22 to −0.25) (four lines in Fig. 2C), and three of four datasets are well-characterized by a single activation energy (0.47 eV) that is slightly lower than the predicted range of 0.6–0.7 eV (95% CI = 0.40–0.54 eV) (three lines in Fig. 2D). The methane seep worm Lamellibrachia sp. (represented by two outlying red symbols in Fig. 2C and D) seems to exhibit lower than expected rates of turnover.

For rockfish, bathymetric distribution data were available that allowed testing average depth as a proxy for POC flux. After accounting for mass and temperature, depth explains significant variation in individual turnover, with deeper rockfish possessing significantly lower rates of turnover (\(F = 4.9, df = 1, 33; P = 0.03\)).

For growth rate, the combined mass-temperature model accounts for significant variation among deep-sea organisms found at depths > 200 m (\(R^2 = 0.28; F = 21.23, df = 2,107; P < 10^{-5}\)). Overall, species grow faster than their larger counterparts on a mass-specific basis. Again, the methane seep worm Lamellibrachia sp. has a comparatively low rate after accounting for size and temperature. Depth does not predict variation in growth rates (\(F = 2.36, df = 1, 106; P = 0.13\)).

Biomass, Abundance, and Body Size. After accounting for spatial autocorrelation, carbon flux, but not temperature, is a significant predictor of body size such that higher fluxes lead to greater average body sizes in a locality (Fig. 3A and Table 1). For

Fig. 1. Sampling locations of bacteria, meiofauna, macrofauna, and megafauna used in the standing stock (yellow triangles) and mollusks used in the diversity analyses (orange circles). Areas shallower than 200 m (i.e., continental shelf) are indicated by pale blue.
abundance and biomass, body size, temperature, and flux are all significant (Fig. 3A and Table 1). Abundance and biomass share similar coefficients, because abundance = biomass/mass; we present both for clarity. Body mass (−1.02; 95% CI = −1.00 to 1.04) scales with abundance at values near MTE predictions of −1 (Eq. S6). For temperature, the coefficient scales (−0.56; 95% eV CI = −0.29 to 0.83 eV) in the opposite direction of the value predicted by MTE (Eqs. S4 and S5). Overall, greater abundances are observed at higher carbon fluxes and among smaller body sizes; the same finding holds true for biomass.

Species Diversity. After accounting for spatial autocorrelation in the data, the quadratic of carbon flux is significant for both Bivalvia and Gastropoda (Fig. 3B and Table 2). Thus, for mollusks, diversity peaks at intermediate chemical energy availability. Temperature does not predict variation in rarefied diversity in any case.

Discussion
The biological responses of organisms living in extreme environments, such as the deep ocean, deserts, and caves, to energy flux have not been well documented. Given the substantial energetic constraints involved, it might be expected that the patterns would differ from more energy-rich environments (31), but communities from extreme habitats may be analogous in their adaptations and response to this mode of life. Among deep-sea benthic organisms, the relative roles of chemical and thermal energy vary considerably across levels of biological organization (Table 3).

At the level of the organism, size and temperature play primary roles in controlling individual metabolic rate and turnover. We find no evidence that the availability of chemical energy influences metabolic rates of deep-sea taxa, consistent with earlier work (32). Likewise, the lack of a role for depth precludes the effect of pressure on metabolic rate, which was previously noted (32). Hydrothermal vent and methane seep organisms experiencing high in situ primary production (orders of magnitude greater than the background abyssal plains) have rates comparable with other deep-sea organisms. The exception seems to be methane seep worms, providing an intriguing avenue of future investigation. We do, however, find some evidence that energy availability, as indexed by depth, influences lifespans of rockfish, perhaps in part because caloric restriction can increase in lifespan (33). Although the size–temperature scaling relationships that we observe for rates of individual metabolism and turnover agree with each other and the predictions of MTE, they differ from those relationships observed for growth rate. These findings are inconsistent, because growth rate is ultimately constrained by metabolic rate and therefore, should exhibit similar scaling. A potential explanation for this discrepancy is that the growth data compiled here include both estimates calculated during some portion of ontogeny and estimates time-averaged over the entire lifespan. Clearly, more work is needed to understand growth rate and its relationship to metabolic rate and lifespan in deep-sea organisms.

Our results suggest that individual metabolic rate proceeds as quickly as allowed by body size and temperature-influenced biochemical kinetics, implying that chemical energy limits biota through its effects at higher levels of biological organization. Variation in carbon flux is the primary driver of patterns in biomass, abundance, and biodiversity. The exception is abundance and biomass, where temperature has a minor but significant role.
Our results indicate that chemical energy plays a primary role in determining spatial patterns of diversity in the deep sea, consistent with other recent studies (22, 39–42). We show that oceanic-scale patterns of biodiversity in the deep sea are directly related to carbon flux. Deep-sea biodiversity exhibits a unimodal relationship with chemical energy availability over both regional (20) and oceanic scales. We do not find that temperature effects scale up to biodiversity patterns, despite hypotheses suggesting a relationship (43) and empirical evidence of its importance in shallow water systems (44). The decline of species diversity with decreased carbon flux may be related to Allee effects, because population numbers decrease under extreme food limitation.

Table 1. Spatially explicit model fits using an SEVM approach for body size, biomass, and abundance (n = 442)

| Variable | Slope coefficient | SE      | t Value | Pr(|t|) | 95% CI Upper | 95% CI Lower |
|----------|-------------------|---------|---------|--------|--------------|--------------|
| Body size | Intercept         | 23.07   | 20.20   | 1.14   | 0.254        | 62.66        | −16.52       |
|          | 1/kT              | −0.85   | 0.48    | −1.78  | 0.0765       | 0.09         | −1.79        |
|          | Ln flux           | 1.17    | 0.26    | 4.61   | 5.31e-06     | 1.68         | 0.66         |
| Biomass  | Intercept         | 20.01   | 5.71    | 3.51   | 0.005        | 31.17        | 8.83         |
|          | Ln mass           | −0.02   | 0.01    | −2.12  | 0.035        | 0.00         | −0.04        |
|          | 1/kT              | −0.56   | 0.14    | 4.15   | 3.96e-05     | −0.29        | −0.83        |
|          | Ln flux           | 0.27    | 0.07    | 3.63   | 0.0003       | 0.41         | 0.13         |
| Abundance| Intercept         | 20.01   | 5.71    | 3.51   | 0.0005       | 31.19        | 8.81         |
|          | Ln mass           | −1.02   | 0.01    | −106.63| <2.00e-16    | −1.00        | −1.04        |
|          | 1/kT              | −0.56   | 0.14    | −4.15  | 3.96e-05     | −0.29        | −0.83        |
|          | Ln flux           | 0.27    | 0.07    | 3.63   | 0.0003       | 0.41         | 0.13         |

Bold values indicated significance at the α = 0.05 level.
with highly oligotrophic regions representing sinks (45). The decline of diversity with increasing carbon flux may reflect guild interactions, where larger mobile deposit feeders monopolize carbon flux while degrading the environment for smaller organisms (40). Intermediate levels of carbon availability may afford a balance between increased species coexistence and decreased niche overlap (46). A considerable amount of variation exists in biodiversity that is not accounted for by the factors here, and it may be related to spatial and temporal variation in environmental factors that are not measured (47, 48).

Despite the deep sea clearly operating under extreme conditions of energy availability, inviting a tendency to regard it as a unique environment, it responds to the same energetic rules as other systems. The deep sea simply represents the extreme end of known processes. Across scales of organization, macroecological patterns in the deep sea are largely consistent with predictions of MTE (4). Across levels, with the notable exception of biodiversity and standing stock, temperature and body size scale near and often encompass MTE predictions for the scaling of mass and temperature. We also find that biological differences among taxa, although significantly elevating or diminishing overall rates, do not change the scaling parameters. The largest inconsistencies with MTE are the lack of temperature scaling in biodiversity and reverse scaling in standing stock. These inconsistencies may result, because a true temperature signal is completely swamped by variation in carbon flux. However, many systems do not exhibit temperature–biodiversity relationships (1, 49). The reverse scaling of temperature with standing stock remains an intriguing finding that warrants additional research.

Previous commentary concluded the prominence of chemical energy as a driving factor for abyssal regions, the deepest, largest, and most food-poor regions of the deep oceans (23). Here, we show that, for the entire deep oceans, the importance of thermal energy prevails at lower levels of biological organization; however, processes and patterns at higher levels are increasingly dominated by chemical energy. Direct effects of body size on these processes may introduce additional indirect effects of chemical energy across biological levels. Thus, climate change will greatly impact ecosystem functioning through impacts on food and temperature regimens operating at different scales of organization. Our findings indicate that the deep sea, once thought to be remote and buffered against climatic change, may function quite differently in the future.

**Methods**

MTE. MTE has attracted both criticism and excitement (50–62). Much of the debate on MTE focuses on aspects of the value of scaling exponents or the importance of fractal networks in predicting scaling with body size (63). Although interesting, these issues are not relevant to this study, because we are less concerned with whether slopes precisely match theoretical predictions. Rather, we use MTE as a useful analytical and hierarchical framework to explore the relative contributions of thermal and chemical energy across scales of biological organization. This application of MTE has proven valuable for explaining variation in a wide range of biological processes (64–67). MTE proposes that individual metabolic rates, by setting the rates of resource uptake from the environment and resource allocation to survival, growth, and reproduction, control ecological processes at all levels of organization from individuals to the biosphere (4). Individual metabolic rate, \( B \) (W), is governed largely by the combined effects of body size, \( M \) (g), and absolute temperature, \( T \) (K), with mass scaling in multiples of 1/4 and temperature scaling near the activation energy of the respiratory complex (∼0.6–0.7 eV) (4). Additional explanation, equations, and predictions across scales of biological complexity can be found in SI Text.

**Data and Analyses.** Datasets were constructed for individual metabolic rates, turnover, and growth as well as biomass, abundance, mean body size, and diversity for communities for a variety of invertebrates and vertebrates inhabiting the shallow and deep oceans. For individual measurements, data were collected on temperature, both in situ and experimental, and body size of the individual. For many of the individual measurements, specific geographic information was not provided that would allow us to derive site-specific estimates of POC flux. As an alternative, we used depth as a proxy for POC. For standing stock and diversity, estimates of in situ temperature and POC flux were used. Specific details of datasets can be found in SI Text, and the data can be found online at [http://dx.doi.org/10.5061/dryad.78nt1](http://dx.doi.org/10.5061/dryad.78nt1).

For metabolic rate, growth rate, and lifespan analyses, we fit linear models using \( R \) statistical software. In explicitly geographic analyses,
applying standard statistical analysis approaches, such as ordinary least squares, can result in spatial autocorrelation remaining in the residuals, leading to increased type I error rates, biased parameter estimates, and spatial pseudoreplication (68). We, therefore, used a spatial eigenvector mapping (SEVM) approach for the size, abundance, biomass, and diversity analyses to explicitly account for the potential effects of spatial autocorrelation on inference (68). Environmental variables were log-transformed and where necessary, centered before incorporation into SEVM models. Linear (biomass, body size, and abundance) and quadratic (diversity) SEVM models were fitted using the R package spdep (http://cran.r-project.org/web/packages/spdep/index.html).

Moran’s I tests indicated that, in contrast to models without the spatial eigenvector components, no significant spatial autocorrelation remained in the residuals of the spatial models, indicating that the SEVM achieved the aim of accounting for spatial autocorrelation.

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Supporting Information

McClain et al. 10.1073/pnas.1208976109

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):

$$B = b_0M^{3/4}e^{-E/(kT-1/kT)},$$

where $M^{3/4}$ describes the body size dependence, $T_1$ is some fixed arbitrary temperature for standardization, and $b_0$ 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 ($8.62 \times 10^{-5}$ eV K$^{-1}$), and $E$ is the activation energy describing the exponential effects of temperature on aerobic metabolism in the respiratory complex ($\sim$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):

$$G \propto B/M = b_0M^{-1/4}e^{-E/(kT-1/kT)}.$$

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),

$$B_{TOT} = N_{TOT}B \propto R,$$

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):

$$N_{TOT} = (B_{TOT}/b_0)M^{-3/4}e^{E/kT} \propto R.$$

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

$$M_{TOT} = N_{TOT}M = (b_0/B_{TOT})M^{1/4}e^{E/kT} \propto R,$$

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),

$$N_{TOT} \propto e^{E/kT}M^{40\log_{10}}/\log_{10}^{3/4},$$

given a predator-to-prey body size ratio $\beta > 1$. This steeper decline arises, because only a small fraction, $\alpha$, of energy is transferred 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 $\beta \sim 10^2$ 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, $N_{TOT}$, for a community comprised of $J$ individuals and $S$ species in an area of size $A$ is equal to $N_{TOT} = J/A$: therefore, the average energy flux per species, $B_{TOT}$, is equal to (Eq. S7)

$$B_{TOT} = BN_{TOT} = BJ/A.$$  

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):

$$S = S_0e^{E/kT},$$

where $S_0 = b_0M^{3/4}/JA_{TOT}$. 

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 $M = M_{TOT}/N_{TOT}$. 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 m$^2$ per tow. Samples span the Atlantic Ocean (Fig. 1). Samples were washed on a 420-μm 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. 51. 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.