

# Energetics of life on the deep seafloor

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**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.**

metabolism | benthos | macroecology | ecosystem function

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  $-1^{\circ}\text{C}$  and  $4^{\circ}\text{C}$  (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 lifespans is unknown. At the community level, biomass and abundance generally decline with depth. Direct tests for the influences 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  $\sim 1\%$  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  $\sim 50\%$  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  $0.12^{\circ}\text{C}$  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

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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 ( $R^2 = 0.44$ ;  $F = 15.69$ , degrees of freedom ( $df$ ) = 2, 40;  $P < 10^{-5}$ ). 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. 2 *A* 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 *Methanoaricia dendrobranchiata*, which seems to have a higher than expected metabolic rate.

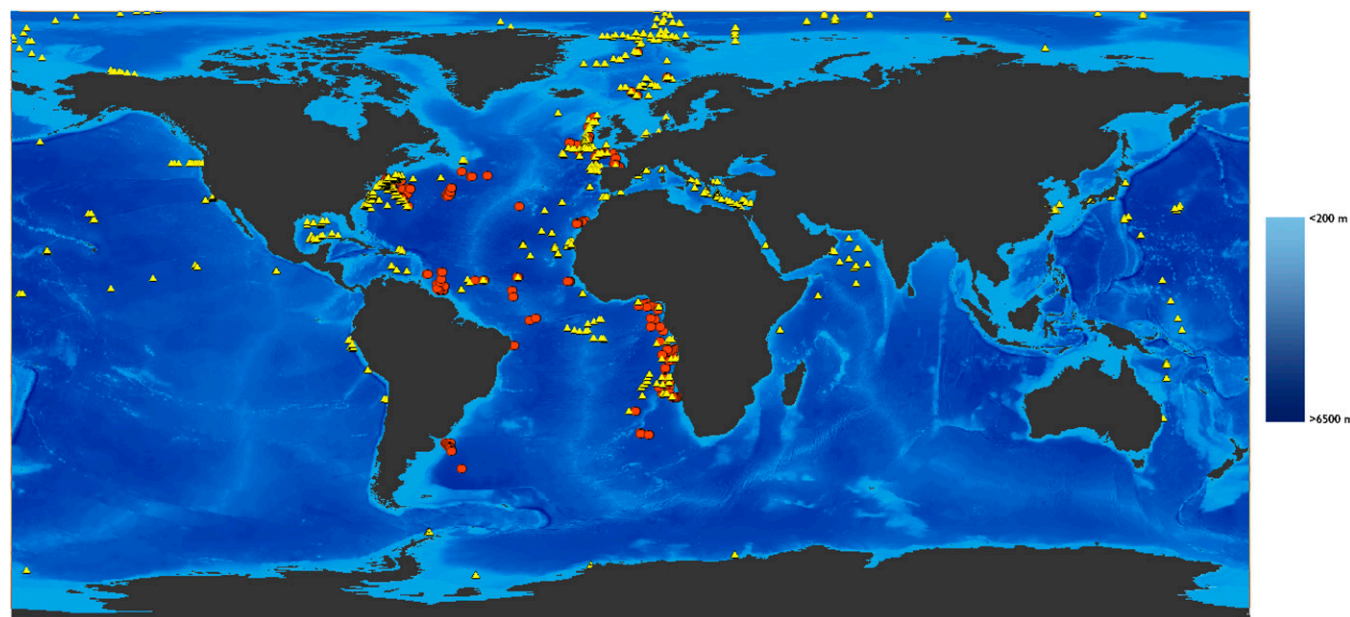
**Individual Turnover and Growth.** For the combined dataset, organisms that are smaller and living at warmer temperatures exhibit higher rates of individual turnover ( $R^2 = 0.91$ ;  $F = 1424$ ,  $df = 2, 291$ ;  $P < 10^{-15}$ ). The 95% CIs for the coefficients encompass MTE-predicted values of  $-0.25$  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. 2 C 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 ( $R^2 = 0.28$ ;  $F = 21.23$ ,  $df = 2, 107$ ;  $P < 10^{-7}$ ; Fig. 2 E and F), although the explanatory power of temperature in the model is marginally nonsignificant ( $F = 3.74$ ,  $df = 1, 107$ ;  $P = 0.06$ ). The mass exponent ( $-0.11$ ; 95% CI:  $-0.14$  to  $-0.07$ ) and activation energy ( $0.16$  eV; 95% CI:  $0.00$ – $0.32$  eV) both differ from the respective values of  $0.25$  and  $0.65$  eV predicted by MTE (Eq. S2). Overall, smaller 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.







Bold values indicated significance at the  $\alpha = 0.05$  level.

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://](http://cran.r-project.org/web/packages/spdep/index.html)

[cran.r-project.org/web/packages/spdep/index.html](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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