Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum

Anastassia M. Makarieva[a,b,1], Victor G. Gorshkov[a,b], Bai-Lian Li[b], Steven L. Chown[c], Peter B. Reich[d], and Valery M. Gavrilov[e]

[a]Theoretical Physics Division, Petersburg Nuclear Physics Institute, Gatchina, St. Petersburg 188300, Russia; [b]Ecological Complexity and Modelling Laboratory, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521; [c]Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa; [d]Department of Forest Resources, University of Minnesota, St. Paul, MN 55108; and [e]Department of Vertebrate Zoology, Moscow State University, Moscow 119992, Russia

Edited by Stephen W. Pacala, Princeton University, Princeton, NJ, and approved July 24, 2008 (received for review March 3, 2008)

A fundamental but unanswered biological question asks how much energy, on average, Earth's different life forms spend per unit mass per unit time to remain alive. Here, using the largest database to date, for 3,006 species that includes most of the range of biological diversity on the planet—from bacteria to elephants, and algae to sapling trees—we show that metabolism displays a striking degree of homeostasis across all of life. We demonstrate that, despite the enormous biochemical, physiological, and ecological differences between the surveyed species that vary over 10^{20}-fold in body mass, mean metabolic rates of major taxonomic groups displayed at physiological rest converge on a narrow range from 0.3 to 9 W kg^{-1}. This 30-fold variation among life's disparate forms represents a remarkably small range compared with the 4,000- to 65,000-fold difference between the mean metabolic rates of the smallest and largest organisms that would be observed if life as a whole conformed to universal quarter-power or third-power allometric scaling laws. The observed broad convergence on a narrow range of basal metabolic rates suggests that organismal designs that fit in this physiological window have been favored by natural selection across all of life's major kingdoms, and that this range might therefore be considered as optimal for living matter as a whole.

allometry | body size | breathing | scaling | energy consumption

The process of life is critically dependent on consumption of energy from the environment. The amount of energy—per unit time per unit mass—required to sustain life can rightfully be considered one of the fundamental questions in biology. Yet a general quantitative answer to this question is lacking, despite the long history and the considerable number of studies devoted to various aspects of organismal energetics in all fields of bioscience. One reason for this persistent knowledge gap is that this fundamental question is typically approached in markedly different ways depending on the organisms being investigated. We show herein how differences in types, protocols, and units of measurements of metabolism have presented a challenge to the development of quantitative generalizations regarding the metabolic rates of organisms. We then use a comprehensive dataset to reconcile such differences and to characterize the remarkable similarity that emerges from comparisons of mass-specific metabolic rates across all of life.

Problem Setting

Studies of animal energetics have frequently focused on the allometric relationship between the whole-body metabolic rate Q and body mass M, $Q = Q_0(M/M_0)^b$, where Q_0 is metabolic rate of an organism with body mass M_0. Either M_0 or Q_0 can be chosen arbitrarily, whereas the second of these parameters is unambiguously defined by the choice of the first one. Usually, M_0 is chosen to be one mass unit—e.g., $M_0 = 1$ g. For the mass-specific metabolic rate $q \equiv Q/M$, we have $q = q_0(M/M_0)^\beta$, $\beta = b - 1$, $q_0 = Q_0/M_0$. Much of the current debate concerns the value of b, and in particular whether it is $\approx$2/3, 3/4, or neither of those (1–9). Because physiological activities like feeding and locomotion profoundly affect animal metabolism, the notion of standard or basal metabolic rate was introduced to obtain comparable results and has become firmly established in animal studies (2, 10). Standard metabolic rate is measured in nongrowing, resting, postabsorptive animals; and in mammals and birds, individuals must be within their thermoneutral zone, in which case the term "basal metabolic rate" is used. When, as in many aquatic animals (9, 11), it is difficult to control for the absence of movement in the studied organism, the routine, rather than standard, metabolic rate is typically measured.

Endogenous metabolic rate—the metabolic rate of nongrowing, unicellular organisms in nutrient-free suspensions (12)—can be considered the microbiological analog of standard metabolic rate in animals. However, whereas in animal studies standard metabolic rate is most frequently reported, studies of endogenous metabolic rate are far less prominent in microbiology. Here, interest has typically been in how fast a given bacterium or fungus can grow on a particular substrate and which conditions can suppress or accelerate this growth (13–15). Accordingly, the majority of published metabolic rates in prokaryotes pertain to growing bacterial cultures. Another important distinction between macro- and micrometabolic studies is that the metabolic rate of microorganisms is normally measured on the bulk mass basis (e.g., oxygen consumption by 1 mg of dry mass of a given species of bacteria) without knowledge of cell size. Whereas in animal studies body mass measurements are a necessity, few studies reporting mass-specific endogenous metabolic rates of bacteria provide an estimate of cell size.

Investigations of metabolic rates in plants recognize the major distinction between photosynthesis, when solar energy is absorbed, carbon dioxide is fixed, and oxygen is produced, and dark respiration, when, like heterotrophs, the photoautotrophic organisms sustain themselves at the expense of internal energy reserves. Plant studies typically measure metabolic rate of the plants' main organs (e.g., leaves and roots), rather than whole organisms (ref. 16, but see ref. 17).

The units in which metabolic rates are reported also differ greatly among groups. For larger animals, metabolic rates are frequently reported per unit total wet mass, whereas for microorganisms,

Author contributions: A.M.M., V.G.G., B.-L.L., S.L.C., P.B.R., and V.M.G. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

[1]To whom correspondence should be addressed. E-mail: elba@peterlink.ru.

This article contains supporting information online at www.pnas.org/cgi/content/full/0802148105/DCSupplemental.

metabolic rates are reported per unit dry mass or per unit mass of cellular carbon, nitrogen, protein, or, in the case of autotrophic microorganisms, chlorophyll *a*. In higher plants, metabolic rate is typically reported per unit leaf dry mass, leaf area, or unit mass of carbon or nitrogen. Because of profound differences in the units of measurements (e.g., milliliters of O_2 consumed per hour by an animal versus millimoles of O_2 consumed per second per mole of chlorophyll *a* by a microalga), no intuitive quantitative comparisons of metabolic rates could be made even by those readers of the biological literature who were crossing the boundaries between the different metabolic research fields.

Given this diversity of approaches, methodologies, and research foci, it is not surprising that the fundamental questions of how much energy, on average, a bacterium, an insect, a mammal, a vascular plant, or an alga spend per unit mass per unit time to remain alive, and how these energy expenditures compare, have not yet received a general answer. Several attempts have been made to compose a quantitative metabolic portrait of life (1, 5, 18). However, these studies have mostly focused on the scaling of metabolic rate, rather than on the absolute magnitudes of metabolic rates; key groups such as prokaryotes, invertebrates, algae, or vascular plants were typically poorly represented; and, finally, unlike the larger animals, the smallest species were included into analyses without controlling for their physiological state. Because metabolic rates of growing unicells are much higher (at least 10–20 times) than endogenous rates, their comparison with the standard metabolic rates of larger species is a source of significant systematic errors in interpreting the dependence of metabolic rate on body size (19–21).

Here, taking these various potentially confounding factors into consideration, we explore variation in the mass-specific metabolic rates supporting living matter at physiological rest, across the widest body size range (20 orders of magnitude) and largest number of species ever analyzed. Of the 3,006 species investigated, the heterotrophic prokaryote *Francisella tularensis*, weighing 10^{-14} g, is the smallest, and the elephant *Elephas maximus*, weighing 4×10^6 g, is the largest.

Because in virtually all species the external energy consumption (feeding in animals, carbon dioxide fixation during photosynthesis in plants) is associated with varying degrees of metabolic rate elevation, we used data only from those studies that report metabolic rates of organisms consuming their own internal energy reserves in the state of minimum activity. These include standard (or, where standard rates were unavailable, routine) metabolic rate in animals, endogenous metabolic rates in unicellular heterotrophs, and dark respiration in photoautotrophs (see *Methods*). Vascular plants are analyzed in three datasets: whole-plant dark respiration in seedlings and in tree saplings and dark respiration of mature green leaves. Inclusion of the latter dataset allows one to control for the growth status of plant tissues (in multicellular plants, some growth points are invariably present, whereas growth ceases in mature leaves) and to specifically determine the energetic demands of the photosynthesizing tissue in the highly differentiated tissue set of higher plants.

In many aquatic organisms, it is difficult to control for the absence of movement that is inherently necessary to adjust the position of the living body in the water column. Therefore, in many taxa, such as crustaceans or cephalopods, the majority of published data correspond to routine metabolic rate (9, 11), rather than to minimal metabolic rate. However, in our analyses among several estimates available for each animal species, we chose the lowest value to obtain as close an estimate of the basal metabolic level as possible. Comparison of taxonomic means with estimates of minimal metabolic rates available for a number of species by means of high-resolution, long-term, real-time metabolic rate measurements (22, 23) indicated that our results for aquatic taxa are fairly close to the minimal rates [supporting information (SI) *Methods* and Table S1], and differences of that magnitude would not alter our overall results or conclusions.

Metabolic rates are strongly influenced by both short- and long-term temperature regimes, so, along with body size, temperature is recognized as a critically important determinant of metabolism in both plants and animals (24–27). Measures of metabolism of widely divergent taxa, as in our study, can be compared at the realized measurement temperature, at a standardized temperature, or at a temperature representative of the *in situ* environment (17), each of which carries its own challenges in terms of interpretation. Given that metabolic rates are not routinely measured at temperatures representative of the *in situ* environment and that respiration is almost always responsive to short-term temperature variation, it seemed prudent to adjust measured values to a standardized temperature. To reconcile measurement temperature differences among studies, we adjusted metabolic rates (see *Methods*) to a common measurement temperature (25°C), except for endothermic vertebrates that do not live at 25°C. The overall range of metabolic rates is somewhat larger if taxa are compared at their measurement, rather than at standardized, temperatures, but the main conclusions of our analyses would be similar if we reported data under measurement rather than standardized temperature conditions.

Results and Discussion

Frequency distributions by taxonomic groups of the log-transformed (wet), mass-specific metabolic rates of the 3,006 species show that the range in mean rates varies 30-fold among groups that include species varying 10^{20}-fold in body mass (Fig. 1 and Table 1). The lowest mean rates, 0.3–0.8 W kg^{-1}, occur in the larger ectothermic taxa and in tree saplings, with higher mean rates, ranging from 1.2 to 8.8 W kg^{-1}, in all other groups, including photoautotrophs and heterotrophs—from prokaryotes to mammals (Table 1). In all taxonomic groups, with the exception of amphibians, reptiles, and tree saplings, at least 15%, and on average 55%, of metabolic rates fall between 1 and 10 W kg^{-1} (Table 1).

The observed 30-fold variation in mean metabolic rates among these disparate life forms is remarkably small compared with the 4,000- to 65,000-fold difference between the mean mass-specific metabolic rates of heterotrophic prokaryotes (mean mass 7×10^{-13} g) and vertebrates (mean mass 2×10^2 g) that should have been observed if life as a whole had conformed to some universal allometric dependence of the type $q = q_0(M/M_0)^{\beta}$, with $\beta = b - 1$ and $b \approx 3/4$ or 2/3 (31) (Fig. 2). Our results exclude the possibility of such a universal dependence (Fig. 2).

Analysis of metabolic scaling within the investigated taxonomic groups (Table 1) supports the contention of recent studies (3, 6–9, 17, 20, 21, 32, 33) that allometry of basal metabolism is an inherent feature of each particular taxon or taxonomic group, rather than commonly shared across taxa. Such variation in allometry has been explored elsewhere, especially in the context of the many factors that might influence such scaling (e.g., ref. 6), and in consequence, we do not explore extensively the basis of such variation here. Nonetheless, a few key points deserve attention. The observed scaling exponents β range from -0.41 in gelatinous invertebrates to 0.37 in heterotrophic prokaryotes (Table 1). The latter dataset is characterized by a relatively narrow range of body masses (Table 1 and Fig. 3); the statistical significance of the metabolic rate dependence on body size in this group arises due to a few points for the larger bacteria and is unlikely to have a biological meaning (20). Conspicuously, all metazoan groups demonstrate a pronounced decline of mass-specific metabolic rates with body mass (Fig. 3), whereas in heterotrophic unicells as well as in all plant groups, the scaling exponents are statistically indistinguishable from zero (Table 1).

Joint consideration of Table 1 and Figs. 1–3 suggests that the relative constancy of mean mass-specific metabolic rate is conserved across diverse taxa in a more fundamental manner than the presence or absence of scaling and the particular value of the scaling exponent. For example, with eukaryotic microalgae lacking scaling

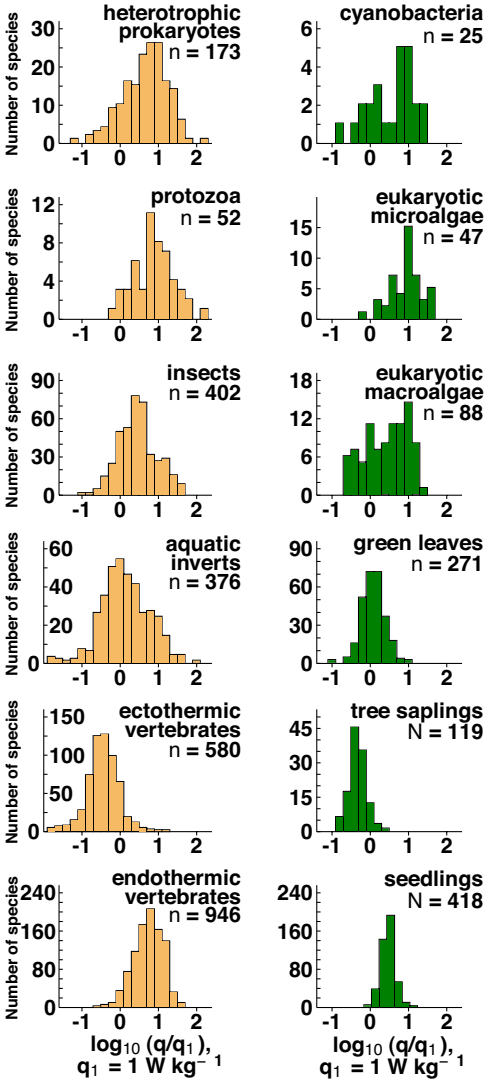

Fig. 1. Frequency distribution of $\log_{10}$-transformed values of mass-specific metabolic rates q (W kg^{-1}) in species differing greatly in size, taxonomy, and trophic status (Table 1). (*Left*) Heterotrophs. (*Right*) Photoautotrophs. Three lowest values falling outside of the 99% C.I. are not shown for aquatic invertebrates. For vascular plants (seedlings and tree saplings), the vertical axis shows number N of individual plants studied.

and endotherms displaying a very pronounced one (Table 1), both groups show a similar unimodal distribution of log-transformed, mass-specific metabolic rates around similar means, and both have >50% of mass-specific metabolic rate within the 1–10 W kg^{-1} interval (Fig. 1 and Table 1). The presence of scaling in endotherms and its absence in the microalgae manifests itself in the fact that in the endotherms the deviations from the group mean correlate with body mass (lower q values are characteristic of larger, and higher values of smaller, species), whereas in the microalgae such correlation is absent.

The available data indicate that the relatively modest 30-fold variation among groups in mean mass-specific metabolic rates can be reduced even further if variation in metabolically inert structural tissues is taken into account in photoautotrophic species. This can be done, as a first approximation, by expressing metabolic rates per unit mass of nitrogen, because the metabolically inert tissues in plants are nitrogen-poor. In trees, for example, an important mechanical function of the nitrogen-poor tissues (wood), which form the bulk mass of stems and branches, is to overcome gravity and distribute the photosynthesizing parts of the plant (leaves) in the three-dimensional space to ensure the maximum light capture. By contrast, aquatic autotrophs do not face this problem; their structural tissues can serve other functions. Accordingly, the photoautotroph species differ significantly in their nitrogen content (nitrogen mass to dry mass ratio). Whereas in many heterotrophs this ratio is in the vicinity of 0.1, in autotrophs it varies from 0.005 in tree saplings [where it decreases with growing tree mass (17)] to 0.06–0.08 in phytoplankton (cyanobacteria and eukaryotic microalgae) (see *SI Methods* and Table S2).

When expressed per unit nitrogen mass from known mean nitrogen content values, autotrophic metabolic rates, which range over 13-fold on a wet mass basis, not only cluster more closely, as has been noted for nitrogen-based plant metabolic rates (17), but also coincide in their range with that of the mean metabolic rates of the majority of heterotroph groups (Table 1). Using the nitrogen-based expression, the range of mean metabolic rates shrinks to (1–4) $\times$ 10^2 W (kg N)$^{-1}$ among all taxa, except the larger ectotherms that still form a separate group with (0.1–0.4) $\times$ 10^2 W (kg N)$^{-1}$ (Table 1), an exception to which we return below. For many groups of animals, coupled data on metabolic rates and nitrogen or dry matter content are scarce, but if available they would help to resolve the nature—random or systematic—of the remaining differences between the mean metabolic rates of the groups studied.

Further refinement of physiological state control in comparisons of metabolic rates of unicells, plants, and small aquatic organisms with those of larger animals would also help resolve the basis of the remaining variation. Endogenous metabolic rates of prokaryotes depend on the age of culture from which the starved cells were originally taken, with a minimum corresponding to the lag phase, a maximum to the exponential phase, and another minimum to the stationary phase, respectively (34–36). Moreover, like the postfeeding metabolic response in animals, prokaryote metabolic rates can decrease substantially with starvation time (see, e.g., ref. 35 and Dataset S1). In autotrophic microorganisms, dark respiration tends to decline with time spent in darkness (37), whereas such changes in vascular plants are modest.

Another challenge in assessing the equivalent of resting state metabolism in higher plants results from the presence of actively growing tissues (such as meristems) in multicellular plants. This may be manifested in the plant data, because with the exception of cyanobacteria and green leaves, the mean values fall within the upper range of the total range (0.4–4) $\times$ 10^2 W (kg N)$^{-1}$ with the maximum of 4 $\times$ 10^2 (W kg N)$^{-1}$ observed in seedlings that presumably grow most actively (Table 1). Mature green leaves with a mean of 2 $\times$ 10^2 (W kg N)$^{-1}$ are closer to the values obtained for adult (i.e., nongrowing) animals. Fine roots have slightly higher mean mass-based and N-based respiration rates than mature leaves (38), but perspective on this comparison must consider that fine roots often include growing tissues and mature leaves do not.

Whatever its nature, the observed 4-fold range of nitrogen-standardized mean mass-specific metabolic rates displayed by major groups of organisms as different in biology as are, for example, insects and trees, or as different in size as are bacteria and mammals (Fig. 3), is remarkably modest. It is truly small compared with the ≈100,000-fold variation in mass-specific metabolic rate displayed by living organisms, from the mean minimum life-supporting metabolic rates registered in organisms in various energy saving regimes—these can be as low as 10^{-2} W kg^{-1} (39)—to the maximum metabolic power output exerted by actively dividing bacteria, flying insects and birds, and jumping vertebrates—these can be well above 10^3 W (kg tissue mass)$^{-1}$ (20, 40). Although a wide variety of metabolic options is biochemically available, the relative majority of species groups have evolved basal or standard rates in the vicinity of 3–9 W kg^{-1} for heterotrophic species (Table 1).

Table 1. Mass-specific metabolic rates q (W kg^{-1}) across life

Taxonomic group	n	N	U	Body mass, g Mean	Min.	Max.	T, °C	q, W kg^{-1} Mean	Lower 95% C.I.	Upper 95% C.I.	% [1–10]	N/DM	q_N, 10^2 W (kg N)$^{-1}$	Allometric scaling α	β (95% C.I.)	R^2	p
Heterotrophs																	
Prokaryotes	**173**	**245**	**D**	**7×10^{-13}**	**1×10^{-14}**	**4×10^{-11}**	**31 (5; 60)**	**4.6**	**0.32**	**68**	**57**	**0.1**	**1.5**	**5.15**	**0.37 (0.23)**	**0.09**	**0.0017**
Protozoa	**52**	**201**	**D**	**1×10^{-8}**	**9×10^{-12}**	**2×10^{-4}**	**20**	**7.5**	**0.71**	**80**	**60**	**0.1**	**2.6**	**0.37**	**−0.06 (0.07)**	**0.05**	**0.095**
Insects	**402**	**402**	**W**	**6×10^{-2}**	**8×10^{-5}**	**7**	**25**	**2.9**	**0.32**	**27**	**67**	**0.1**	**1.0**	**0.25**	**−0.18 (0.04)**	**0.19**	**$<10^{-5}$**
Aquatic invertebrates	**376**	**989**	**W**	**9×10^{-2}**	**3×10^{-6}**	**1×10^{4}**	**11 (−1.7; 32)**	**1.3**	**0.07**	**26**	**49**	**0.1**	**0.4**	**−0.09**	**−0.21 (0.03)**	**0.41**	**$<10^{-5}$**
Crustacea: copepods and krill	138	314	W	2×10^{-3}	3×10^{-6}	6	13 (−1; 30)	3.0	0.23	39	56	0.1	1.0	−0.36	−0.30 (0.06)	0.46	$<10^{-5}$
Crustacea: peracarids	86	226	W	7×10^{-2}	8×10^{-5}	5×10^{1}	12 (−1.5; 30)	1.4	0.06	29	57	0.1	0.4	−0.21	−0.28 (0.12)	0.21	10^{-5}
Crustacea: decapods	80	197	W	5	5×10^{-4}	9×10^{2}	13 (−1.7; 30)	0.56	0.05	6	33	0.1	0.2	−0.05	−0.31 (0.09)	0.37	$<10^{-5}$
Mollusca: cephalopods	38	218	W	4×10^{1}	1×10^{-3}	1×10^{4}	5	0.78	0.03	21	42	0.1	0.3	0.18	−0.18 (0.14)	0.16	0.014
Gelatinous invertebrates	34	34	W	2×10^{-1}	2×10^{-3}	2×10^{1}	5 (1; 15)	0.78	0.18	3.5	35	0.1	0.3	−1.05	−0.41 (0.08)	0.77	$<10^{-5}$
Ectothermic vertebrates	**580**	**7,498**	**W**	**3×10^{2}**	**2×10^{-2}**	**3×10^{4}**	**19 (−1.5; 45)**	**0.36**	**0.06**	**2.3**	**11**	**0.1**	**0.1**	**−0.21**	**−0.17 (0.03)**	**0.18**	**$<10^{-5}$**
Amphibians	158	682	W	8	2×10^{-1}	7×10^{2}	19 (4; 35)	0.39	0.09	1.6	9	0.1	0.1	−0.26	−0.16 (0.06)	0.16	$<10^{-5}$
Fish	266	6,333	W	4×10^{2}	2×10^{-2}	7×10^{3}	14 (−1.5; 30)	0.38	0.04	3.2	15	0.1	0.1	−0.19	−0.15 (0.05)	0.11	$<10^{-5}$
Reptiles	156	483	W	7×10^{2}	4×10^{-1}	3×10^{4}	26 (5; 45)	0.30	0.06	1.6	7	0.1	0.1	−0.13	−0.22 (0.04)	0.43	$<10^{-5}$
Endothermic vertebrates	**946**	**1,327**	**W**	**1×10^{2}**	**3**	**4×10^{6}**	**38**	**5.5**	**1.0**	**30**	**72**	**0.1**	**1.8**	**1.42**	**−0.31 (0.01)**	**0.75**	**$<10^{-5}$**
Birds	321	321	W	9×10^{1}	3	1×10^{5}	39	8.7	2.0	37	51	0.1	2.9	1.59	−0.34 (0.02)	0.84	$<10^{-5}$
Mammals	625	1,006	W	2×10^{2}	3	4×10^{6}	37	4.4	0.87	22	83	0.1	1.5	1.30	−0.29 (0.01)	0.76	$<10^{-5}$
Photoautotrophs																	
Cyanobacteria	**25**	**75**	**D**	**2×10^{-11}**	**7×10^{-13}**	**6×10^{-9}**	**26 (2; 45)**	**3.7**	**0.24**	**58**	**60**	**0.06**	**2.1**	**1.73**	**0.12 (0.30)**	**0.03**	**0.46**
Eukaryotic microalgae	**47**	**193**	**C**	**9×10^{-10}**	**6×10^{-12}**	**6×10^{-6}**	**15 (0.5; 20)**	**8.8**	**1.3**	**58**	**51**	**0.08**	**3.7**	**0.85**	**−0.01 (0.09)**	**0.00**	**0.76**
Eukaryotic macroalgae	**88**	**106**	**D**	**n.d.**	**n.d.**	**n.d.**	**8 (0; 30)**	**2.1**	**0.19**	**36**	**57**	**0.02**	**3.2**	**n.d.**	**n.d.**	**n.d.**	**n.d.**
Vascular plants: green leaves	**271**	**271**	**D**	**n.a.**	**n.a.**	**n.a.**	**25**	**1.2**	**0.31**	**4.6**	**61**	**0.02**	**2.0**	**n.a.**	**n.a.**	**n.a.**	**n.a.**
Vascular plants: tree saplings	**4**	**119**	**D**	**70**	**0.7**	**2×10^{3}**	**24**	**0.51**	**0.19**	**1.4**	**6**	**0.005**	**3.4**	**1.09**	**0.02 (0.02)**	**0.00**	**0.19**
Vascular plants: seedlings	**42**	**418**	**D**	**8×10^{-1}**	**3×10^{-2}**	**7×10^{1}**	**24**	**3.6**	**1.6**	**8.3**	**99**	**0.03**	**4.0**	**0.15**	**0.06 (0.06)**	**0.03**	**0.054**

n, number of species; N, number of data entries analyzed (statistics are based on N in seedlings and tree saplings and on n in all other groups); U, dominant mass units in the original data sources—metabolic rates reported mostly per dry (D), wet (W), or carbon (C) mass basis; for body mass, geometric mean, minimum, and maximum values in the group are shown; in seedlings and tree saplings, wet mass was estimated from dry mass data assuming a 30% dry mass to wet mass ratio; n.d., not determined; n.a., not applicable; T, mean and range of measurement temperatures in the data sources, and in endotherms mean body temperature from ref. 7. ''Copepods and krill'' comprise 85 copepod and 9 krill species, as well as 7 similarly sized branchiopods and 2 *Balanus* spp. ''Peracarids'' include amphipods, isopods, mysids, 2 cumaceans, as well as five (nonperacarid) ostracod species. ''Gelatinous invertebrates'' comprise medusae (28) and chaetognaths (29). ''Cyanobacteria'' include unicellular, filamentous and mat-forming species. ''Eukaryotic microalgae'' comprise diatoms, dinoflagellates, haptophytes, and unicellular chlorophytes; eukaryotic filaments are included in ''Eukaryotic macroalgae''. Rows in boldface correspond to panels in Fig. 1. For mass-specific metabolic rate q, the geometric mean and 95% C.I. (assuming log-normal distribution) are shown; % [1–10] is percentage, in each group, of mass-specific metabolic rate values falling at or between 1 and 10 W kg^{-1}; gelatinous medusae and chaetognaths have DM/WM ratio significantly smaller [by 7 and 3 times, respectively (11, 30)] than the crude mean DM/WM = 0.3 for the nongelatinous groups, their wet-mass-based metabolic rates were multiplied by a factor of 7 and 3, respectively, to be comparable with the rest of the database; N/DM is nitrogen mass to dry matter mass ratio, N/DM = 0.1 is a crude mean for the heterotrophic groups studied (Table S2); q_N is mean metabolic rate per unit nitrogen mass. All nonendothermic metabolic rates were converted to 25°C prior to analysis (see *Methods*). In the last 3 columns, parameters of ordinary least squares regression $\log_{10} q = \alpha + \beta \log_{10} M$, where q is in W kg^{-1} and M is in g, are given; R^2 and p are the squared correlation coefficient and significance level, respectively.

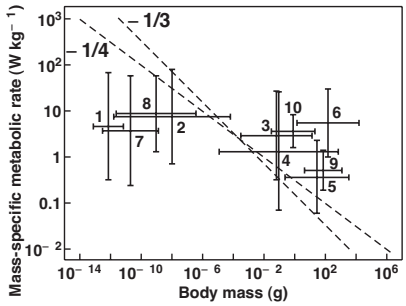

Fig. 2. Mean mass-specific metabolic rates q versus mean body mass M in the studied groups of organisms. Squares correspond to mean body mass and mean mass-specific metabolic rate in each group (Table 1); horizontal and vertical bars show 95% C.I. of body mass and mass-specific metabolic rate values, respectively, within each group. 1, heterotrophic prokaryotes; 2, heterotrophic protozoa; 3, insects; 4, aquatic invertebrates; 5, ectothermic vertebrates; 6, endothermic vertebrates; 7, cyanobacteria; 8, eukaryotic microalgae; 9, tree saplings; 10, tree seedlings. The dashed lines marked −1/4 and −1/3 describe the dependence $q = q_0(M/M_0)^{\beta}$, where $\beta = -1/4$ or −1/3, respectively, and M_0 = 0.2 mg and q_0 = 2.6 W kg^{-1} are the unweighted averages of mean body masses and mean mass-specific metabolic rates of each group. Note that neither of the lines describes the studied dataset.

The Metabolic Optimum Perspective

Convergence on a relatively narrow range in the basic costs of living across such a wide variety of life forms establishes grounds for introducing and scrutinizing the concept of metabolic optimum (41). Within the present context, it can be defined as the range of metabolic rates that maximizes the evolutionary and long-term ecological success of the organism—i.e., metabolically optimal species have been favored by natural selection against those whose metabolic rates depart substantially from the optimum. The challenge is thus to find quantitative indicators of evolutionary and ecological success that could be used for analyzing the possible linkage between the intrinsic metabolic rate of a given species and its level of performance in the ecosystem. Apparently, one such indicator could be the share of the ecosystem-level energy flux claimed by the considered organisms.

From this perspective, it is noteworthy that life's most important energy flux—primary productivity—is ensured by living beings

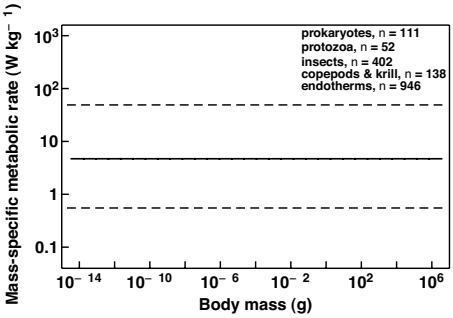

Fig. 3. Body mass range of heterotrophic species that keep their mean taxonomic mass-specific metabolic rate within the proposed metabolic optimum of 1–4 × 10^2 W (kg N)$^{-1}$ or 3–9 W (kg wet mass)$^{-1}$ (Table 1); n is the number of species shown. This range harbors organisms of practically all sizes found on Earth. Aquatic invertebrates with body mass $M \gg 10^{-3}$ g and ectothermic vertebrates have lower metabolic rates outside of this range (Table 1) presumably because of the breathing costs' limitation (*SI Appendix*). A solid line and two dashed lines indicate the unweighted averages of the mean mass-specific metabolic rate (4.7 W kg^{-1}) and the upper and lower 95% C.I. (0.51 and 49 W kg^{-1}), respectively, across the five groups (Table 1). Species number of prokaryotes is less than in Table 1 because cell size estimates were unavailable for some species.

that, in the basal state, all function near the optimal metabolic rate, be they blue-green algae, eukaryotic phytoplankton, macroalgae, or trees (Table 1). The most important consumers of this flux, prokaryotes, which can consume up to 95% of primary productivity in stable ecosystems (42), are also characterized by this optimal rate. The most abundant invertebrates on land (insects) and in the ocean [copepods (11)], which claim the second largest share of the biosphere's energy flux after the unicells (42), metabolize at the optimal rate also. Thus, at physiological rest the biosphere appears to run on average predominantly at the optimal rate. More detailed analyses of ecosystem-level energy consumption rates of similarly sized taxonomic groups inhabiting similar ecological niches (e.g., reptiles versus mammals) could shed more light on the correlation of the proposed metabolic optimality and ecological dominance.

At the organismal level, the notion of metabolic optimum appears to provide a unifying theoretical explanation for such ubiquitous and seemingly unrelated features of life organization as animal breathing and the flat morphology of green leaves. Passive diffusion delivers oxygen at a size-independent rate f per unit body surface area S and, in the case of geometric similarity, $S \propto M^{2/3}$, would make the mass-specific metabolic rate scale as $q \propto fS/M \propto M^{-1/3}$. Given the established 95% C.I. for the metabolic optimum ranges from ≈0.5 to 50 W kg^{-1} (Fig. 3) and starting from q = 50 W kg^{-1} at $M \sim 10^{-12}$ g (mean body mass of prokaryotes satisfying their oxygen demands with diffusion), we conclude that the diffusion-based metabolic scaling would drive the mean mass-specific metabolic rate outside of the optimal 95% C.I. at a body mass of ≈10^{-6} g. This is the predicted value of the critical body size at which animals should have evolved active mechanical breathing to elevate the oxygen flux f above the diffusion-based value and to return their mass-specific metabolic rate back into the optimal metabolic interval. This prediction is matched by the data: the smallest animal in this study has body mass of 3 × 10^{-6} g (Table 1), and there are few animals much smaller than 10^{-6} g (see also Fig. 2).

Mechanical breathing involves certain energetic costs associated with the movement of the breathing organs. As simple physical considerations show, the share of the organismal energy budget spent on breathing grows with increasing body size, with increasing mass-specific metabolic rate, and with decreasing ambient oxygen concentration (*SI Appendix*). Large animals in an oxygen-poor environment (e.g., water) spend a greater share of their energy budget on breathing than do small animals in an oxygen-rich environment (e.g., air). At sufficiently large body sizes, the maintenance of a size-independent mass-specific metabolic rate becomes physically prohibited, because the breathing costs would exceed the total metabolic rate of the animal. By using the available data, the critical body size for aquatic animals has been estimated at ≈1 mm and body mass at ≈1 mg (*SI Appendix*). This energetic limitation might explain the observed departure of the larger aquatic taxa of ectotherms as well as of all ectothermic vertebrates from the proposed metabolic optimum range (Table 1 and Figs. 1–3).

In plants, the available flux of solar energy f_s delivered per unit leaf surface area does not depend on leaf functioning and limits the mass-specific metabolic rate q of the leaf as $q \leq f_s S/M$, where S is leaf area and M is its mass. A way for the leaves to remain within the metabolic optimum range is to keep the ratio SLA $\equiv S/M$ (specific leaf area) large (and leaf thickness $l \propto 1/\mathrm{SLA}$ small) at any leaf mass M. This conditions the flat shape of the green leaf, which has volume $V = d^2 l \propto M$ and diameter d much greater than thickness l, $d \gg l$, the latter rarely exceeding 10^{-3} m. At $M \propto d^2 l$ and $d \gg l$, leaf mass and leaf thickness become practically independent. This also explains why the mass-specific respiration q of the green leaves is associated with SLA (43) and, hence, with l, but, unlike in animal bodies, appears to be independent of mass M (44).

Conclusions

We have demonstrated that across dramatically different life forms, mean mass-specific metabolic rates converge on a relatively narrow range that is striking in contrast to the 20 orders of magnitude difference in the body mass of the studied species. This remarkable and previously unappreciated phenomenon is likely associated with the pervasive biochemical universality of living matter. It thus becomes a biochemical challenge to determine the specific biochemical processes that are responsible for the observed broad metabolic convergence at the level of cell functioning (45). There are many other important questions to be addressed that are beyond the scope of this data compilation. Many of these involve temperature. For instance, do differences in thermal adaptation and acclimation within and among major taxonomic groups contribute to the narrow window of realized metabolic rates or make the window appear larger than it would otherwise be? Because the ordered process of energy consumption is what ultimately distinguishes living matter from the nonliving, it can be hoped that the metabolic regularities presented in our analysis can shed new light on questions such as this, and more broadly on the principles of life's organization.

Methods

The database comprising mass-specific metabolic rates of 3,006 aerobic species was compiled by literature search. Where a few values for one and the same species were available, the lowest value was taken. Only in seedlings and saplings of vascular plants were all of the available data analyzed, because they present a range of body masses comparable with that observed in other taxonomic groups.

Oxygen consumption rates were converted to power units by using 20 J $(\text{ml } O_2)^{-1}$, which involves a major assumption that the anaerobic energy generation is negligible. To noticeably alter the results obtained, the applied oxygen energetic equivalent should have been changing in a systematic manner by hundreds of percent across taxa; this differs sharply from the relative constancy of oxygen energetic equivalent revealed in comparisons of direct and indirect calorimetry (46, 47). Metabolic rates reported on the dry mass basis [q_{DM}, W $(\text{kg DM})^{-1}$] were converted to wet mass basis (q, W kg^{-1}) assuming a mean 30% dry matter content: $q = q_{DM} \times 0.3$. The value of 30% was chosen as a crude mean for the variable DM/WM ratio in the nongelatinous heterotrophic groups where metabolic rate was reported on wet mass basis (*SI Methods* and Table S3). Mass-specific metabolic rate per unit nitrogen mass, q_N, is related to q as $q_N = q/(\text{DM/WM})/(\text{N/DM})$, where N/DM is the nitrogen mass to dry mass ratio. For each group, the value of q_N in the last column of Table 1 was calculated using the mean value of q, the corresponding N/DM ratio, and DM/WM = 0.3. Nonendothermic q values obtained at different temperatures T (°C) were transformed to 25°C, $q_{25} = q \times Q_{10}^{(25-T)/(10°C)}$, using Q_{10} = 1.65, 2.21, and 2.44 for fish, amphibians, and reptiles, respectively (7); Q_{10} = 2.5 for cephalopods (9); Q_{10} = 1.4 for macroalgae as determined for species studied here (Dataset S9); a variable Q_{10} based on measurement temperature for higher plants and leaves (17, 25); and $Q_{10} = 2$ for other ectotherm groups (8, 19, 48, 49). No temperature adjustments of metabolic rates were performed for endothermic vertebrates that do not live at body temperatures of 25°C. All data and further details of data conversions are presented in Datasets S1–S11, *SI Methods*, and Tables S1–S3.

ACKNOWLEDGMENTS. S.L.C. thanks Elrike Marais and John Terblanche for assistance. We thank two anonymous referees for their excellent critiques. This work was partially supported by the National Science Foundation and the University of California Agricultural Experiment Station (B.-L.L.), the National Science Foundation and the Wilderness Research Foundation (P.B.R.), and the Rainforest Concern and Global Canopy Program (A.M.M. and V.G.G.).

1. Hemmingsen AM (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep Steno Mem Hosp* 9:1–110.
2. Peters RH (1983) *The Ecological Implications of Body Size* (Cambridge Univ Press, Cambridge, UK).
3. Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *J Anim Ecol* 68:893–905.
4. Darveau C-A, Suarez RK, Andrews RD, Hochachka PW (2002) Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature* 417:166–170.
5. Brown JH, *et al.* (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
6. Glazier DS (2005) Beyond the ''3/4-power law'': Variation in the intra- and interspecific scaling of metabolic rate in animals. *Biol Rev* 80:611–662.
7. White CR, Phillips NR, Seymour RS (2006) The scaling and temperature dependence of vertebrate metabolism. *Biol Lett* 2:125–127.
8. Chown SL, *et al.* (2007) Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Funct Ecol* 21:282–290.
9. Seibel BA (2007) On the depth and scale of metabolic rate variation: Scaling of oxygen consumption rates and enzymatic activity in the Class Cephalopoda (Mollusca). *J Exp Biol* 210:1–11.
10. McNab BK (1997) On the utility of uniformity in the definition of basal rates of metabolism. *Physiol Zool* 70:718–720.
11. Ikeda T, Skjoldal HR (1989) Metabolism and elemental composition of zooplankton from the Barents Sea during early Arctic summer. *Mar Biol* 100:173–183.
12. Dawes EA, Ribbons DW (1964) Some aspects of the endogenous metabolism of bacteria. *Bacteriol Rev* 28:126–149.
13. Haddock BA, Jones CW (1977) Bacterial respiration. *Bacteriol Rev* 41:47–99.
14. Russell JB, Cook GM (1995) Energetics of bacterial growth: Balance of anabolic and catabolic reactions. *Microbiol Rev* 59:48–62.
15. McDonnell G, Russell AD (1999) Antiseptics and disinfectants: Activity, action, and resistance. *Clin Microbiol Rev* 12:147–179.
16. Wright IJ, *et al.* (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827.
17. Reich PB, Tjoelker MG, Machado J-L, Oleksyn J (2006) Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature* 439:457–461.
18. Robinson WR, Peters RH, Zimmermann J (1983) The effects of body size and temperature on metabolic rate of organisms. *Can J Zool* 61:281–288.
19. Fenchel TB, Finlay J (1983) Respiration rates in heterotrophic, free-living protozoa. *Microb Ecol* 9:99–122.
20. Makarieva AM, Gorshkov VG, Li B-L (2005) Energetics of the smallest: Do bacteria breathe at the same rate as whales? *Proc R Soc London Ser B* 272:2325–2328.
21. Makarieva AM, Gorshkov VG, Li B-L (2005) Biochemical universality of living matter and its metabolic implications. *Funct Ecol* 19:547–557.
22. Kawall HG, Torres JT, Geiger SP (2001) Effects of the ice-edge bloom and season on the metabolism of copepods in the Weddell Sea, Antarctica. *Hydrobiology* 453/454:67–77.
23. Steffensen JF (2002) Metabolic cold adaptation of polar fish based on measurements of aerobic oxygen consumption: Fact or artefact? Artefact! *Comp Biochem Physiol* 132:789–795.
24. Cossins AR, Bowler K (1987) *Temperature Biology of Animals* (Chapman & Hall, New York).
25. Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends Plants Sci* 8:343–351.
26. Clarke A (2004) Is there a universal temperature dependence of metabolism? *Funct Ecol* 18:252–256.
27. Atkin OA, Bruhn D, Hurry VM, Tjoelker MG (2005) The hot and the cold: Unravelling the variable response of plant respiration to temperature. *Funct Plant Biol* 32:87–105.
28. Thuesen EV, Childress JJ (1994) Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. *Biol Bull* 187:84–98.
29. Thuesen EV, Childress JJ (1993) Enzymatic activities and metabolic rates of pelagic chaetognaths: Lack of depth-related declines. *Limnol Oceanogr* 38:935–948.
30. Hirst AG, Lucas CH (1998) Salinity influences body weight quantification in the scyphomedusa Aurelia aurita: Important implications for body weight determination in gelatinous zooplankton. *Mar Ecol Prog Ser* 165:259–269.
31. Hoppeler H, Weibel ER (2005) Editorial. Scaling functions to body size: Theories and facts. *J Exp Biol* 208:1573–1574.
32. Makarieva AM, Gorshkov VG, Li B-L (2003) A note on metabolic rate dependence on body size in plants and animals. *J Theor Biol* 221:301–307.
33. Gavrilov VM (1997) *Energetics and Avian behavior*, Physiology and General Biology Reviews (Harwood Academic, Amsterdam), Vol 11.
34. Feofilova EP, Lebedeva NE, Taptykova SD, Kirillova NF (1966) Study on respiration of pigmented and leuco-variants of Actinomyces longispororuber. *Mikrobiologiya* 35:651–659.
35. Burleigh IG, Dawes EA (1967) Studies on the endogenous metabolism and senescence of starved Sarcina lutea. *Biochem J* 102:236–250.
36. Palese LL, *et al.* (2003) Characterization of plasma membrane respiratory chain and ATPase in the actinomycete Nonomuraea sp ATCC 39727. *FEMS Microbiol Lett* 228:233–239.
37. Geider RJ, Osborne BA (1989) Respiration and microalgal growth: A review of the quantitative relationship between dark respiration and growth. *New Phytol* 112:327–394.
38. Reich PB, *et al.* (2008) Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecol Lett* 11:793–801.
39. Makarieva AM, Gorshkov VG, Li B-L, Chown SL (2006) Size- and temperature-independence of minimum life-supporting metabolic rates. *Funct Ecol* 20:83–96.
40. Suarez RK (1996) Upper limits to mass-specific metabolic rates. *Annu Rev Physiol* 58:583–605.
41. Gorshkov VG (1981) The distribution of energy flow among the organisms of different dimensions. *Zh Obshch Biol* 42:417–429.
42. Makarieva AM, Gorshkov VG, Li B-L (2004) Body size, energy consumption and allometric scaling: A new dimension in the diversity-stability debate. *Ecol Complexity* 1:139–175.
43. Reich PB, *et al.* (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: A test across biomes and functional groups. *Oecologia* 114:471–482.
44. Reich PB (2001) Body size, geometry, longevity and metabolism: Do plant leaves behave like animal bodies? *Trends Ecol Evol* 16:674–680.
45. Hochachka PW, Somero GN (2002) *Biochemical Adaptation: Mechanism and Process in Physiological Evolution* (Oxford Univ Press, Oxford).
46. Walsberg GE, Hoffman TCE (2005) Direct calorimetry reveals large errors in respirometric estimates of energy expenditure. *J Exp Biol* 208:1035–1043.
47. Walsberg GE, Hoffman TCE (2006) Using direct calorimetry to test the accuracy of indirect calorimetry in an ectotherm. *Phys Biochem Zool* 79:830–835.
48. Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Mar Biol* 139:587–596.
49. Vladimirova IG, Zotin AI (1985) Dependence of metabolic rate in Protozoa on body temperature and weight. *Zh Obshch Biol* 46:165–173.