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Energetics of the smallest:

Do bacteria breathe at the same rate as whales?

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Summary

Power laws describing the dependence of metabolic rate on body mass have been established for many taxa, but not for prokaryotes, despite the ecological dominance of the smallest living beings. Our analysis of 80 prokaryote species with cell volumes ranging more than 1,000,000-fold revealed no significant relationship between mass-specific metabolic rate q and cell mass. By absolute values, mean endogenous mass-specific metabolic rates of non-growing bacteria are similar to basal rates of eukaryote unicells, terrestrial arthropods and mammals. Maximum mass-specific metabolic rates displayed by growing bacteria are close to the record tissue-specific metabolic rates of insects, amphibia, birds and mammals. Minimum mass-specific metabolic rates of prokaryotes coincide with those of larger organisms in various energy-saving regimes: sit-and-wait strategists in arthropods, poikilotherms surviving anoxia, hibernating mammals. These observations suggest a size-independent value around which the mass-specific metabolic rates vary bounded by universal upper and lower limits in all body size intervals.

Keywords: prokaryotes, eukaryotes, metabolic rate, endogenous, scaling

Running head: Metabolic rates of prokaryotes

1. Introduction

There is currently a widening recognition of the ecological importance of the smallest living beings (Horner-Devine *et al*. 2003; Nee 2004). Indeed, bacteria were found to dominate and control the ecosystem energy flow consuming more than 90% of primary productivity in stable ecosystems on land as well as in the ocean and freshwater bodies (Gorshkov 1981, 1995; del Giorgio *et al*. 1997; Biddanda *et al*. 2001; Makarieva *et al*. 2004). In spite of the apparent significance of prokaryote metabolic rate patterns for ecological theory, until now, except for five species of bacteria of undefined physiological state analyzed by Hemmingsen (1960), no attempts have been made to relate metabolic rates of prokaryote cells to cell size and compare prokaryote metabolism with that of larger organisms.

Within all taxa so far studied (Peters 1983), including unicellular eukaryotes (Fenchel & Finlay 1983; Vladimirova & Zotin 1983), mass-specific metabolic rate q (W kg^{-1}) declines with growing body mass M as $q \propto M^{\alpha}$. Extending this scaling relationship to the whole domain of life at $\alpha = -1/4$ (Gillooly *et al*. 2001) predicts that prokaryotes, as the smallest living beings, should feature highest mass-specific metabolic rates exceeding those of the largest organisms by thousands of times. Here we analyze data on metabolic rates of a total of 80 prokaryote species to find that, contrary to this prediction, on a mass-specific basis bacteria metabolize at rates similar to those of much larger organisms, including the largest animals inhabiting the biosphere.

2. Methods

As revealed by analysis of unicellular eukaryotes (Fenchel & Finlay 1983), metabolism of unicells varies greatly with growth conditions. This makes consideration of cells of undefined physiological state of only limited interest and demands that physiological state be taken into account in any allometric analysis (Fenchel & Finlay 1983). In the higher organisms it is common to measure standard metabolic rate, which pertains to adult (i.e. non-growing), post-absorptive animals in the state of minimum activity (Peters 1983). In prokaryotes, viability of non-growing cells in the absence of exogenous substrates is supported by the so-

called endogenous metabolism, which, similar to standard metabolism of animals, corresponds to consumption of internal energy reserves (Dawes & Ribbons 1963). To account, in the first approximation, for the physiological differences in prokaryote metabolism, we collected two separate datasets on endogenous (n = 56) and growth (n = 55) metabolism for a total of 80 prokaryote species (38 *Proteobacteria*, 22 *Firmicutes*, 12 *Cyanobacteria*, 5 *Actinobacteria*, 1 spirochaete, and 2 *Archaea*). Mean cell volumes of the studied species ranged from 1.4×10^{-2} to 2×10^{4} μm^{3}.

Many prokaryote species survive one-two days of starvation with no loss of viability defined as the ability to form colonies (Sobek *et al*. 1966; Ensign 1970; Robertson & Batt 1973). If starved for longer periods, prokaryotes either irreversibly lose viability or switch off life processes taking highly resistant forms (e.g., spores). The negligible respiration characteristic of such inactive physiological states (Desser & Broda 1965; Ramaiah *et al*. 2002) can be interpreted as slow spontaneous degradation of organic matter and apparently bear little relevance to metabolic rates supporting viable cells. In our dataset the time of resource deprivation after which endogenous metabolic rate was monitored did not normally exceed one day.

Published metabolic rates were converted to W (kg wet mass)$^{-1}$ using dry to wet mass ratio of 0.2 (Clarholm & Rosswall 1980; Otte *et al*. 1999) and protein to dry mass ratio of 0.5 (Stal & Moezelaar 1997; Otte *et al*. 1999). Aerobic oxidation of endogenous substrates was assumed to yield 20 J (ml O_2)$^{-1}$ (Robertson *et al*. 1983). Energy yields of anoxic fermentation of the endogenous glucose by five species of cyanobacteria and a few chemolithothrophic reactions performed by *Thioploca araucae* and *Thiovulum majus* were taken from Gnaiger (1983) and Kelly (1991), respectively. Where direct measurements of cell mass were unavailable, cell mass was estimated from linear dimensions reported by Holt (1984, 1986, 1989) and several other authoritative sources assuming 1 g ml^{-1}, following the procedure adopted by Fenchel & Finlay (1983) in their analysis of metabolic allometry in unicellular eukaryotes. Complete dataset and details of calculations are presented in the Appendix.

3. Results

3.1. Absolute values of mass-specific metabolic rates in prokaryotes

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No statistically significant dependence of either endogenous or growth mass-specific metabolic rate q on cell mass M was revealed. Results of the ordinary least-square regression of log-transformed values, $\log_{10} (q/q_0)$ $= a + b \log_{10} (M/M_0)$, $q_0 = 1$ W kg^{-1}, $M_0 = 10^{-12}$ g, are as follows: $a = 0.58 \pm 0.30$, $b = -0.18 \pm 0.26$ ($\pm$ 95% C.I.), $r^2 = 0.07$, $p = 0.048$, $n = 56$ for endogenous mass-specific metabolic rate and $a = 1.84 \pm 0.22$, $b = 0.09$ ± 0.23 ($\pm$ 95% C.I.), $r^2 = 0.03$, $p = 0.22$, $n = 55$ for mass-specific metabolic rate during growth.

These results pertain to temperature-uncorrected values of mass-specific metabolic rates. Robinson *et al*. (1983) established that the exponential temperature term in the dependence of metabolic rate on temperature is statistically insignificant for interspecific comparisons among 67 species of unicells. (The conclusion about a significant temperature term across species of unicells was reached by Gillooly *et al*. (2001) based on analysis of 29 observations for nine species only, i.e. for a data set heavily biased towards intraspecific comparisons.) In our dataset the mean temperature of metabolic rate measurements in the studied prokaryote species was $T = 30 \pm 9$ °C ($\pm$ 1 S.D.) for endogenous metabolism and $T = 32 \pm 8$ °C for growth metabolism, Table 1. To confirm the expected absence of a temperature effect, we corrected mass-specific metabolic rates to reference temperature $T_0 = 37$°C (310 °K) using temperature-correction factor $e^{-E/RT} = e^{-8000 \, °K/T}$, where $R = 8.31$ J (mol)$^{-1}$ (°K)$^{-1}$ is gas constant (Boltzmann's constant multiplied by Avogadro number) and the value of activation constant E was chosen to be 66.58 kJ (mol)$^{-1}$ as in Brown *et al*. (2004). Temperature-corrected values $q(T_0)$ were obtained from values $q(T)$ measured at temperature T (degrees Kelvin) as

$$q(T_0) = \exp\left(\frac{8000 \, °K}{T} - \frac{8000 \, °K}{T_0} \right) q(T) . \qquad (1)$$

Logarithmic slopes b for the temperature-corrected values were $b = -0.05 \pm 0.27$ ($\pm$ 95% C.I.) ($r^2 = 0.01$, $p = 0.57$) for endogenous metabolism and $b = +0.25 \pm 0.27$ ($\pm$ 95% C.I.) ($r^2 = 0.13$, $p = 0.007$) for growth metabolism. As expected, temperature correction did not change the initial conclusion about absence of slopes statistically different from zero.

Compared to prokaryotes, unicellular eukaryotes display clearer patterns. Fenchel & Finlay (1983) analyzed 134 metabolic rate measurements for a total of 44 protozoans (amoebae, ciliates and flagellates), classifying the physiological state of the cells as growing, starved or unspecified. We calculated from their data that for endogenous mass-specific metabolic rate of starved cells (31 observations, 10 species, 20 °C) the ordinary least-square regression intercept is $a = 1.92 \pm 0.54$ ($\pm$ 95% C.I.) and the slope is $b = -0.26 \pm 0.11$ ($\pm$ 95% C.I.) ($r^2 = 0.60$, $p < 10^{-5}$). For growing cells (58 observations, 9 species) the intercept is $a = 3.00 \pm 0.63$ ($\pm$ 95% C.I.) and the slope is $b = -0.36 \pm 0.13$ ($\pm$ 95% C.I.) ($r^2 = 0.58$, $p < 10^{-5}$). It should be noted, however, that the dataset of Fenchel & Finlay (1983) was formed excluding the data which were considered "unrealistic" by the authors. It is therefore possible that the dataset is to some extent biased towards those values which fall more or less closely to the expected Hemmingsen's curves discussed by Fenchel & Finlay (1983). For comparison, Vladimirova & Zotin (1983) report 205 measurements of endogenous metabolic rates for 50 protozoan species (and a total of 554 observations for 108 species collected from 320 published sources). For this dataset with no selectivity in data collection the observed patterns are less pronounced and the slope b for endogenous mass-specific metabolic rate is less negative: $a = 1.12 \pm 0.23$ ($\pm$ 95% C.I.) and $b = -0.10 \pm 0.06$ ($\pm$ 95% C.I.) ($r^2 = 0.11$, $p < 10^{-5}$) (all reported intercepts are equal to the decimal logarithm of mass-specific metabolic rates (W kg^{-1}) at 10^{-12} g).

Possible correlation between prokaryote q and M in our dataset could be masked by several factors warranting further investigation, including culture history and cell density, nature and time of resource deprivation and uncertainties associated with determination of cell size. Changing physiological state is likely to be another disturbing factor: First, cell size can change conspicuously depending on the growth phase, and, second, mass-specific endogenous respiration of bacteria immediately after resource deprivation can be several times higher than the stabilized endogenous respiration of cells starved for a longer while (Sobek et al. 1966; Christensen et al. 1980). A similar host of factors was discussed by Fenchel & Finlay (1983), but in prokaryotes the situation is aggravated by their minute size, corresponding to 10,000-100,000 times difference in body mass between bacteria and average-sized protozoa. The small size increases the

uncertainties of cell size and other measurements. In this light it is remarkable that in the dataset of Vladimirova & Zotin (1983), where the correlation coefficient is low, the mean mass of cells is $3,300 \times 10^{-12}$ g. This is almost an order of magnitude lower, Table 1, than in the dataset of Fenchel & Finlay (1983), where the correlation coefficient in the relationship of metabolic rate on cell size is much higher. Fenchel & Finlay (1983) proposed that if more detailed information on physiological state of the studied cultures is provided in future studies, this may result in clearer and more significant allometric relationships between metabolic rate and cell size in protozoa. This is likely to be true for prokaryotes as well and opens the way for more refined analyses.

At the current stage the main message of Figure 1 is therefore contained in the absolute values of the observed metabolic rates. These absolute values are not affected by the way individual cell size is estimated, as they are measured on the bulk basis (e.g. oxygen consumption by 1 mg dry mass of a given species of bacteria) without involving the knowledge of individual cell size. Growth metabolic rates of prokaryote species studied range from 7 to 3000 (geometric mean 70) W kg^{-1}, with 56% observations falling between 10 and 100 W kg^{-1}, Table 1. Endogenous mass-specific metabolic rates range from 0.08 to 37 (geometric mean 3.3) W kg^{-1}, with 45% of observations falling between 1 and 10 W kg^{-1}, Table 1.

3.2. Lower and upper limits to metabolism of prokaryotes and other organisms
As a whole, prokaryotes display a four orders of magnitude scatter in the observed mass-specific metabolic rates, Figure 1, from approx. 10^{-1} to 10^3 W kg^{-1}. In order to explore the universality of these boundaries we compared them with the minimum and maximum metabolic rates found in larger organisms. We collected data on mass-specific metabolic rates of organisms in various energy-saving regimes. Singer *et al.* (1993) established that mass-specific metabolic rates of mammals hibernating at lower body temperatures are independent of body mass and constitute the lower limit to mammalian metabolism at around 10^{-1} W kg^{-1}. Along with hibernating animals, we also considered mass-specific metabolic rates of sit-and-wait strategists like, e.g., scorpions and ticks (Lighton *et al.* 2001) (able to thrive for years without food) and of various

poikilotherms under anoxic conditions. Metabolic depression during anoxia is an important physiological mechanism allowing the animals to adapt ecologically to environments characterized by fluctuating oxygen availability (Guppy *et al*. 1994) (e.g., intertidal ecosystems). For our data set (a total of 73 species) we observed a mass-independent value of q_{MIN} = 0.20±0.02 (± 1 S.E.) W kg^{-1}, Figure 1. Anoxic metabolic rates were consistently lower than aerobic ones, 0.07±0.02 versus 0.25±0.02 and 0.22±0.03 (± 1 S.E.) W kg^{-1} in hibernators and sit-and-wait strategists, respectively.

Ten lowest values of endogenous metabolic rate in prokaryotes (mean T = 27 °C) with a mean of 0.23±0.04 (± 1 S.E.) W kg^{-1} fall remarkably close to the q_{MIN} value determined for the higher organisms in energy-saving regimes, Figure 1. Among these ten values one comes from a starved soil bacterium ecologically adapted to survive prolonged periods of unfavorable conditions (Ensign 1970) and five pertain to anoxic fermentation in cyanobacteria (Stal & Moezelaar 1997). This gives further credit to the ecological and physiological meaningfulness of q_{MIN} (Gorshkov 1981; Singer *et al*. 1993; Makarieva *et al*. 2003).

Record maximum metabolic rates per unit working tissue mass exhibited during flight of some insects and hummingbirds as well as during the highest jumps of insects, amphibians and mammals (a total of 24 species with body masses ranging over 10,000,000-fold), appear to be of the order of one to a few thousand W kg^{-1}, close to the maximum mass-specific metabolic rates found in growing prokaryotes and to the estimated metabolic rate for the fastest observed cell divisions in bacteria (doubling time less than 20 min), Figure 1. These record values with a mean of $(2.1±0.4 \ (± \ 1 \ \text{S.E.}))×10^3$ W kg^{-1} presumably characterize the biochemical upper limit q_{MAX} to metabolism of the living matter (Suarez 1996).

Discussion

These findings indicate that the mass-specific metabolic rates of living cells vary within universal limits that are on a large scale independent of the size of the organism to which they belong. The particular value of metabolic rate displayed by a cell appears to be more a function of the biochemical properties of the corresponding tissue and of the physiological and ecological status of the organism rather than be dictated by body size. For example, in humans mass-specific metabolic rate of brain tissue is 33 times higher than that of

skin (Aiello & Wheeler 1995), while in insects mass-specific metabolic rates of flight muscles can be 150 times higher during flight than at rest (Josephson *et al.* 2001). For mean whole-body mass-specific metabolic rates such metabolic scopes would correspond to more than a million-fold range of body masses. Yet these scopes can be observed within one and the same organism. Metabolic power laws established for different taxa (Peters 1983) should be therefore profoundly affected by the allometry of tissue composition of the living bodies (i.e. the changing ratio of metabolically active to inactive tissues) (Oikawa & Itazawa 2003). Similarly, differences in characteristic tissue biochemistry (mitochondrial efficiency, volume density, membrane permeability, etc.) may account for the existence of taxa with different standard metabolic rates within one and the same body size interval (Lighton *et al.* 2001; Darveau *et al.* 2002). For example, among the largest animals (body size exceeding 1 g) reptiles and other poikilotherms display several times' lower metabolic rates than mammals and birds of comparable size and body temperature (Peters 1983); among animals of "intermediate" size (from 10^{-5}-10^{-4} to 1-10 g) ticks and scorpions have metabolic rates four to seven times lower than "typical" arthropods (Lighton *et al.* 2001), Figure 1; finally, among the smallest organisms like unicells there also likely to be taxa characterized by similarly low metabolic rates, Figure 1, however, here the relevant taxonomic information is still scarce.

Metabolic power laws are commonly established for evolutionarily close organisms (Peters 1983) and usually pertain to a body mass range of about five-six orders of magnitude. In the meantime, comparative analysis of mass-specific metabolic rates across the whole domain of life, i.e. over 20 orders of magnitude change in body mass, reveals a large degree of similarity between mean mass-specific metabolic rates observed in organisms from dramatically different body size intervals. By absolute values, endogenous mass-specific metabolic rates of bacteria are very similar to basal metabolic rates of mammals, Figure 1. About 20% of the species studied have endogenous mass-specific metabolic rates even lower than the basal rates of whales and elephants, the largest animals with measured metabolic rates, Figure 1.

This result rules out the existence of the proposed universal scaling law valid across the entire domain of life (Gillooly *et al.* 2001). An elephant with body mass $M_1 = 3.7 \times 10^6$ g has a basal mass-specific metabolic rate $q_1 = 0.6$ W kg^{-1} (Heusner 1991) and a body temperature of around $T_1 = 37$ °C. If there existed a

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universal scaling law $q \propto M^{-1/4}e^{-E/RT}$ (Gillooly *et al*. 2001) at $E = 66.58$ kJ (mol)$^{-1}$ (Brown *et al*. 2004) this would mean that at $T_2 = 30$ °C a bacterium with $M_2 = 10^{-12}$ g should have respired at a rate $q_2 = q_1 \times (M_1/M_2)^{1/4}\exp(8000/T_1 - 8000/T_2) = 14{,}500$ W kg^{-1}. This predicted value differs by more than one thousand times from the observed mean endogenous mass-specific metabolic rate of prokaryotes, Table 1. The smallest species in our dataset, a firmicute *Acholeplasma laidlawii*, has a body mass of 10^{-14} g and endogenous metabolic rate of 0.9 W kg^{-1} at 37 °C. This is only 1.5 times higher than the basal mass-specific metabolic rate of the elephant, instead of being 140,000 times higher as predicted from $q \propto M^{-1/4}e^{-E/RT}$, if applied universally.

Is there, on the other hand, any universal absolute value of mass-specific metabolic rate, which would be common to different-sized taxa? Mammalian species numbers peak at $M \approx 300$ g (May 1978). This body size corresponds to basal metabolic rate of around 4 W kg^{-1}, Figure 1. Species numbers in terrestrial arthropods peak between 0.1 and 1 mg (Morse *et al*. 1988; Ulrich 2004), which again corresponds to $q \approx 4$ W kg^{-1} at 25° C (Lighton *et al*. 2001), Figure 1. These estimates are largely insensitive to the actual body size corresponding to maximum species numbers within each size interval. For example, in terrestrial arthropods $q \propto M^{-0.14}$ (Lighton *et al*. 2001), which means that a 1,000-fold error in body mass estimate would correspond to less than a threefold error in metabolic rate estimate. It thus appears that standard mass-specific metabolic rates displayed by the majority of terrestrial species in body size intervals from about 10^{-5} g to 1 g and from 1 g to 10^8 g approximately coincide. Moreover, they come close to the mean endogenous mass-specific metabolic rate of prokaryotes (geometric mean 3 W kg^{-1}) ranging in size from 10^{-14} to 10^{-8} g. Interestingly, dark respiration of plant leaves is characterized by similar rates: around 2 W kg^{-1} in conifers, 6 W kg^{-1} in broad-leaved trees and 12 W kg^{-1} in forbs (Reich *et al*. 1998) (over 60 species, 25 °C). These rates are directly comparable to mean endogenous metabolic rates of different prokaryote phyla, Table 1. Mean endogenous respiration of unicellular eukaryotes studied by Vladimirova & Zotin (1983) is again similar, with a geometric mean of 6 W kg^{-1}, arithmetic mean of 12 W kg^{-1}, Table 1, and 54% of observations falling between 1 and 10 W kg^{-1}. An independent analysis of endogenous respiration of unicellular eukaryotes by

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Fenchel & Finlay (1983) produces a similar result, Table 1. For their data set the geometric mean for endogenous respiration is also 6 W kg^{-1} and 45% of observations fall between 1 and 10 W kg^{-1}. These comparisons pertain to temperatures close to characteristic natural ambient temperatures of existence for the taxa studied (except for bacteria, where 30 °C is an overestimate for free-living species).

These analyses highlight the biochemical universality of living matter, which appears to require a uniform rate of energy supply per unit mass for its maintenance, largely independent of the size of the organism it constitutes (Makarieva *et al*. 2005a,b). This makes it possible to discuss a universal metabolic optimum favored by natural selection in diverse taxa, Figure 1. With growing body size and decreasing surface-to-volume ratio, the organisms have to perfect their mechanisms of energy uptake from the environment, as well as their distributive networks, in order to maintain the rate of energy supply of their cells at the optimum level. By comparing ecosystem energy fluxes claimed under natural conditions by organisms of similar size, but featuring different mass-specific metabolic rates (e.g., reptiles versus mammals; ticks versus beetles, etc.) it would be possible to reveal whether particular values of mass-specific metabolic rate are associated with ecological energetic dominance.

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LEGENDS TO FIGURE AND TABLE

Figure 1. Limits and scopes of mass-specific metabolic rate in the living organisms.

Solid and open circles: endogenous and growth mass-specific metabolic rates of prokaryotes. **Boxes, diamonds and triangles (MIN):** metabolic rates of eukaryotes in various energy-saving regimes. **Dotted circles (MAX):** record mass-specific metabolic rates per unit working tissue mass during peak activities in various organisms. **Asterisks:** basal metabolic rates of whales and elephants. **Solid lines:** fitted equations for endogenous/standard/basal metabolic rate in **U** unicellular eukaryotes at 20 °C (Vladimirova & Zotin 1983), **A** terrestrial arthropods at 25 °C (Lighton *et al.* 2001), and **M** mammals (Peters 1983), respectively. **Crossed circles:** standard metabolic rate corresponding to body size class with maximum species numbers in terrestrial arthropods and mammals; mean endogenous respiration of the studied prokaryotes and unicellular eukaryotes (Vladimirova & Zotin 1983). **Dashed lines:** the uniform minimum, maximum and hypothesized optimum values of mass-specific metabolic rate of the living matter. Numeric values and literature sources for all points shown in the figure are given in the Appendix.

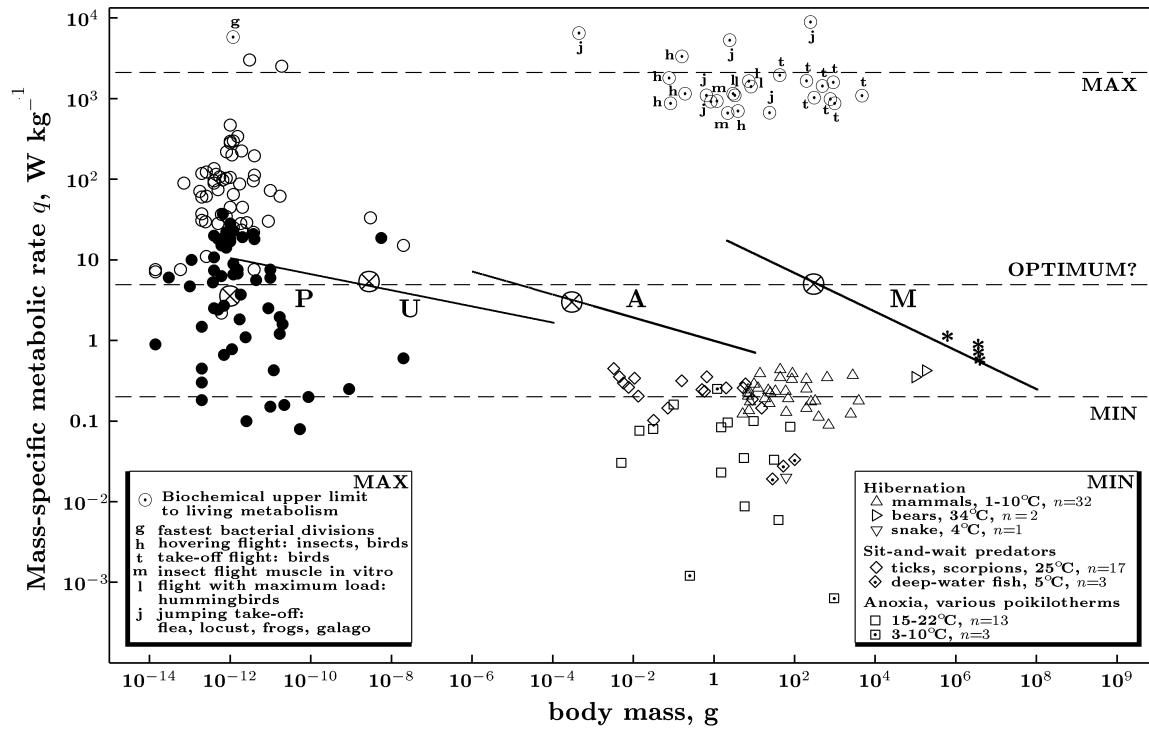Table 1. Metabolic rates in prokaryotes and unicellular eukaryotes, *n* is the number of species studied.

Fig. 1

Table 1.

Taxonomic group	n	Metabolic rate q, W kg^{-1}			Cell mass, 10^{-12} g			Temperature, °C
		Mean	Min	Max	Mean*	Min	Max	
Prokaryote endogenous								
Proteobacteria	27	11	0.3	37	1.8	0.2	20,000	27 (10…37)
Cyanobacteria	12	3	0.08	19	28	0.7	5,600	26 (19…39)
Firmicutes	11	8	0.18	22	0.35	0.014	3.7	32 (21…37)
Actinobacteria	4	3	0.1	11	0.8	0.2	2.5	34 (30…37)
Archaea	2	14	10	17	0.3	0.11	1	60
All species	56	8	0.08	37	2.1	0.014	20,000	30 (10…60)
Prokaryote growth								
Proteobacteria	28	320	15	3000	2.6	0.2	20,000	27 (10…37)
Firmicutes	21	64	7.1	218	0.4	0.014	3.8	35 (30…50)
Actinobacteria	4	74	31	107	0.3	0.2	0.5	35 (30…37)
Spirochaetes	1	89	89	89	0.07	0.07	0.07	30
Archaea	1	49	49	49	1	1	1	60
All species	55	190	7.1	3000	1	0.014	20,000	32 (10…60)
Protozoa endogenous								
Data of Vladimirova & Zotin (1983) [§]	50	12	0.2	94	3,300	7	224,000,000	20
Data of Fenchel & Finlay (1983) [†]	10	10	0.6	37	30,400	25	27,600,000	20
Protozoa growth								
Data of Fenchel & Finlay (1983) [‡]	9	57	0.3	623	40,100	50	71,000,000	20

*Geometric mean; [§]statistics for 205 measurements; [†]statistics for 31 measurements; [‡] statistics for 58 measurements.