NOTE

FURTHER EVIDENCE FOR ANOMALOUS SIZE SCALING OF RESPIRATION IN PHYTOPLANKTON[1]

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ABSTRACT

Respiration per unit mass decreases as organism size increases among metazoans and heterotrophic unicells. The rate of decrease is described by a power function of organism mass; the exponent of the power function is 0.75 (Three-fourths Rule). Previously unanalyzed respiration rates for 11 species of phytoplankton ranging in size over four orders of magnitude show a size-scaling exponent of 1.13 (SE, ±0.15), which is statistically different from 0.75. This result confirms the result of an earlier study of eight phytoplankton species indicating that size scaling of respiration is absent or minimal in phytoplankton, in contrast to the pattern of heterotrophic unicells. The size-related range of respiration rates per unit mass across the full size spectrum of phytoplankton would be approximately 18-fold if respiration were scaled according to the Three-fourths Rule. If respiration does not scale with size or scales minimally with size, as suggested by present evidence, the size-related range of rates will be much smaller or negligible. The apparent anomaly of size scaling for phytoplankton respiration is potentially of great ecological and adaptive significance in unicellular algae.

Key index words: algal energetics; allometry; phytoplankton respiration; phytoplankton size; size scaling

Relationships between size and metabolic rate have been extensively studied for metazoans, especially vertebrates (Peters 1983). The long-recognized decrease in specific metabolic rate with increasing size has typically been considered allometric ($R = aM^b$, where R is respiration of an organism per unit time and M is mass: Brody 1945). An early and recurrent hypothesis concerning this relationship is that the allometric exponent tends toward 0.67, reflecting the size-related change in ratio of surface area to volume for any fixed shape. However, this so-called "Surface Law" was questioned by Kleiber (1932) on empirical grounds. For vertebrates, Kleiber found a better fit to the exponent 0.75. Zeuthen (1947, 1953) showed that the exponent 0.75 was applicable to a wide size range of nonvertebrate metazoans and unicells. Zeuthen's work was subsequently confirmed for a larger data base by Hemmingsen (1960). Because of the apparent convergence of exponents on 0.75 over moist size ranges for most major groups

of organisms, the allometric relationship between size and respiration has come to be known as the Three-fourths Rule (or Kleiber's Rule). This rule, which is actually a statistical generalization rather than a physiological law, has withstood some recent critical scrutiny (Heusner 1982, Feldman and McMahon 1983): 0.75 still appears to be the exponent most representative of the relationship between mass and metabolic rate.

For unicellular organisms, the information base has been and remains much less satisfactory than for metazoans (Robinson et al. 1983). Zeuthen (1947) included unicells ranging in size from bacteria to large protozoans and marine invertebrate eggs in his broad empirical synopsis of nonvertebrate respiration rates. Zeuthen concluded that the allometric exponent for unicells was 0.7. Hemmingsen (1960) subsequently provided better documentation of the relationship among unicells, for which he derived an exponent of 0.75 (SE, ±0.02). These studies indicated that unicells would conform to the Three-fourths Rule.

Despite its general importance, the size-metabolism relationship has not been well established for phytoplankton, which are dominant primary producers in marine and fresh waters. The work of Zeuthen and of Hemmingsen that led to the confirmation of the Three-fourths Rule for unicells did not include any data on autotrophic unicells.

The respiration rates of phytoplankton in relation to size were first dealt with specifically by Laws (1975) on the basis of data collected by Eppley and Sloan (1965). For phytoplankton respiration, Laws calculated an allometric exponent of 0.69 ± .06. From this he concluded that phytoplankton conformed to the Surface Law. However, given the breadth of the standard error, his analysis could not actually serve as a basis for distinctions between the Surface Law (0.67) and the Three-fourths Rule (0.76).

The analysis of Laws was criticized by Banse (1976), who rederived the relationship from the same respiration rates using size estimates from the primary data source rather than estimates based on a general equation, as Laws had done. Banse's treatment of the data showed an exponent of 0.90 (eight species, range 20–7000 pg wet mass; 95% confidence interval 0.79–1.02). Eppley (1977) later obtained a similarly high coefficient for the same data (0.93). The exponent obtained by Banse deviates significantly
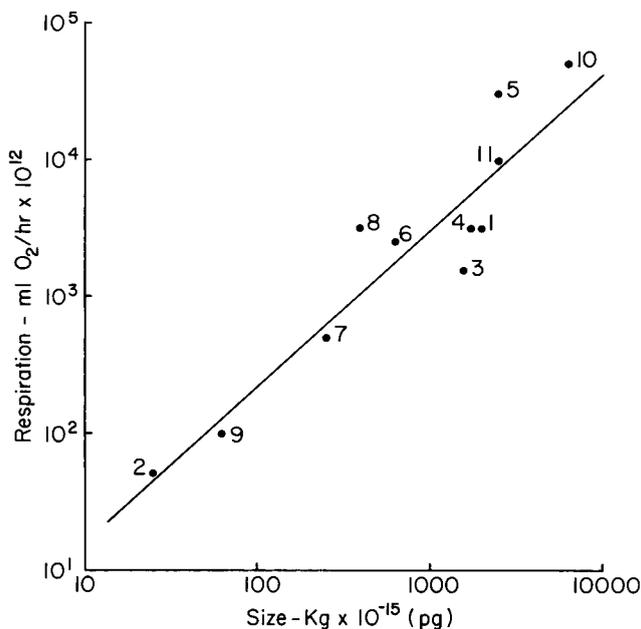
FIG. 1. Relationship between size and respiration for eleven phytoplankton species reported by Brown and Richardson (1968): *Cyanidium caldarum* (1), *Gloeocapsa alpicola* (2), *Phormidium luridum* (3), *Phormidium persicinum* (4), *Astasia longa* (5), *Amphidinium* sp. (6), *Nitzschia closterium* (7), *Ochromonas danica* (8), *Chlorella pyrenoidosa* (9), *Chlorococcum wimmeri* (10), *Euglena gracilis* (11).

However, Robinson et al. did not make a separate analysis of the phytoplankton data, which were pooled with more abundant data for unicellular heterotrophs.

The emphasis of the study by Brown and Richardson was change of metabolism and pigment composition in relation to light for unicellular algae. The paper contains information on dark respiration and size for 11 species, most of which are freshwater planktonic forms. Cell volumes were measured with a particle counter; for present purposes it is assumed that one μm^3 of cell volume equals 1 pg wet mass. Dark respiration was measured in cultures grown at a variety of irradiances. The respiration rate for cultures grown at moderate light intensities (600 ft-candles) is used here. Respiration rates at higher irradiances were not analyzed because high irradiances may induce high rates of light respiration that extend for a considerate interval into the dark respiration phase (e.g. Olesen and Ganf 1986).

Figure 1 shows a log–log plot of the size and respiration data from Brown and Richardson (1968). As expected, respiration increases with increasing mass; the rate of increase tells whether the specific respiration rate (respiration per unit mass) increases (slope >1), decreases (slope <1), or remains more or less the same (slope $= 1$) over the size spectrum. The slope of the least squares best fit to the log–log relationship shown in Figure 1 is 1.13 (SE, ± 0.15). Thus, the allometric equation is as follows: $R = 1.48 \times 10^{-5} M^{1.13}$, where R is expressed as mL $O_2 \cdot h^{-1}$ and M is expressed as kg fresh mass (these units are the most common ones for scaling studies, but power units may be preferable: one watt is approximately equal to 180 mL $O_2 \cdot h^{-1}$). The fit of the points to the log–log relationship is excellent ($R = 0.92; P < 0.01$).

The allometric exponent is greater than 1.0, which would indicate an increase rather than a decrease in the oxygen consumption per unit mass with increasing size. However, the allometric exponent is not statistically different from 1.0 and therefore is consistent with no size scaling, minimal size scaling, or moderately inverse size scaling of respiration. The exponent does differ significantly from 0.75, however, and thus is consistent with Banse's finding of an unexpectedly high exponent for phytoplankton respiration.

The scaling exponent for the data set from Brown and Richardson might well be lower if size were expressed as carbon rather than wet mass. Direct carbon measurements are unavailable. Equations have often been used in estimating carbon from wet mass or cell volume (Strathmann 1967). The applicability of these equations to the taxa studied by Brown and Richardson is unknown and may be questionable in the lower size ranges, for which Strathmann's non-diatom equation predicts dry mass approaching 50% of wet mass. If Strathmann's nondiatom equation is used, the value of the ex-

from the expected exponent based on the Three-fourths Rule (0.75); it suggests minimal size scaling or no size scaling of respiration over a wide range of phytoplankton sizes. However, the exponent is based on data for only a few species.

Only a few small data sets have been analyzed for size scaling of respiration since Banse's treatment of the data from Eppley and Sloan. Falkowski and Owens (1978), working with six marine taxa spanning a size range of 10–1000 pgC·cell^{-1}, found no evidence for size scaling of respiration. Blasco et al. (1982), who measured respiratory electron transport activity in six species of marine diatoms (77–62 $\times$ 10^5 $\mu m^3 \cdot$cell^{-1}), documented an exponent significantly above 0.75 for size scaling based upon carbon (b = 0.91, 95% confidence limits, 0.88–0.94). The exponent was lower (0.77) when cell volume was used as the index of size, but cell volume is not a reliable indicator of protoplasm volume for marine diatoms because a large portion of the cell may be accounted for by vacuole space. The data of Blasco et al. may not be comparable to most other data because respiration was measured under continuous irradiance.

An unanalyzed data set can be found in the work of Brown and Richardson (1968). The data from this study, although collected for other purposes, are reasonably well-suited for comparison of size and respiration. The data of Brown and Richardson were included as part of the respiration scaling analysis by Robinson et al. (1983) for unicells in general.

ponent declines to 0.86, but the standard error increases to 0.18, and the exponent is still not statistically different from 1.0.

It remains impossible to reach a firm conclusion concerning the size scaling of respiration in phytoplankton because of the small number of species that have thus far been studied and the necessity of using data that were not specifically obtained for the purpose of size-scaling analysis. However, the data presently suggest that respiration in phytoplankton is either unscaled or minimally scaled in relation to cell size. If this is the case, phytoplankton cells provide a major contrast with heterotrophic unicells and small metazoans, both of which conform to the Three-fourths Rule.

The net production and survival of phytoplankton are affected to a significant extent by energy loss during intervals when photosynthesis is not possible, i.e. at night or at times when cells are situated below the euphotic zone. Because the Three-fourths Rule has been assumed to apply to phytoplankton, large cells have been considered to have lower maintenance demands than small cells (Laws 1975), which would in turn imply longer survival times for large cells in the absence of light (Ramberg 1979). In addition, size scaling of metabolism may influence trophic interactions (Banse 1982).

The respiration per unit mass of the smallest phytoplankton taxa (ca. 1 pg wet mass) would be approximately 18 times as great as that of the largest phytoplankton taxa (ca. 10^5 pg wet mass) if the Three-fourths Rule were applicable. However, if respiration does not scale with size, there will be no difference in the respiration rates of small and large cells on a unit mass basis. Uniformity of respiration rates has considerable adaptive and ecological significance.

For most groups of organisms, respiration is likely to be a major selective force influencing organism size because small organisms will be committed to much higher maintenance losses than large organisms. In the absence of a relationship between size and respiration, size selection will be dependent entirely on other size-related factors, such as nutrient uptake or vulnerability to grazing. At the community level, lack of size scaling implies lack of respiration parity with heterotrophs, especially among the largest and the smallest organisms, for which the rates are most extreme. Lack of respiration parity may confer size-related advantages or disadvantages upon phytoplankton in relation to heterotrophs (cf. Banse 1982). Size-related shifts in relative maintenance demands of unicellular autotrophs and heterotrophs could influence the structure and organization of plankton communities. Thus, the present evidence indicating deviation of the phytoplankton from the Three-fourths Rule has major implications for the modelling and interpretation of phytoplankton populations and communities in nature.

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