

MINIREVIEW

NEW LIGHT ON THE SCALING OF METABOLIC RATE WITH THE SIZE OF ALGAE

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The scaling of metabolic rate with the size of algae has been discussed and researched at length. The observation that algae usually have exponents b in the equation $R = a \cdot W^{-b}$ (where R is the specific growth rate, W is the organism [cell] biomass, and a and b are constants) equal to or higher than the value of -0.25 for many other organisms is generally related to resource-saturated (maximal) values of R . Recent work has shown that the exponent b for light-limited growth is more negative than -0.25 . This was predicted from considerations of the package effect in photon absorption, as modulated by the volume-specific pigment content of the cells, and the photosynthetic unit size. Further work is needed to extrapolate these findings to fluctuating light environments. This minireview puts the recent work into a broader context and suggests how further work could quantify the roles of optical thickness and of spatial and temporal variations in the radiation field in determining metabolic rates.

Key index words: cell size; fluctuating irradiance; light-limited growth; package effect; pigment content; specific growth rate

Biologists have long been interested in the size of organisms as determinants of their metabolic and growth rates, their ecology, and their biodiversity (Haldane 1928, Pirie 1973, May 1989). Phycologists have contributed data on, and interpretations of, these functional considerations of the size of organisms (see Banse 1982, Raven 1986, 1998, 1999a,b, Chisholm 1992). Most data on metabolic and growth rates of algae refer to measurements under resource-saturated conditions (Banse 1982, Chisholm 1992, Raven 1999b), although there are data for resource-limited growth rates, such as a limited supply of PAR (e.g. Schlesinger et al. 1981).

Although many attempts have been made to make quantitative mechanistic interpretations of the size-dependent variations in metabolic and growth rates of

algae, there is still uncertainty as to the nature of the relationship between metabolic and growth rates and the size of organisms and the mechanistic basis of this relationship (or relationships). General aspects of the size of algal organisms are considered before we deal with recent advances.

CELL AND ORGANISM SIZE AND ALGAL FUNCTION

The volume of cells among phytoplankton organisms species over a range of some 10^{11} -fold, and this range is only reduced to 10^{10} -fold if prokaryotes are excluded. The volume-based ranges are only reduced by one or two orders of magnitude when referred to on a dry matter or carbon basis (Raven 1986, 1998, 1999a,b, Chisholm 1992).

Physics and physical chemistry show that this range of sizes has very significant influences on phytoplankton performance. The simplest case to examine is that of spherical cells and colonies. An increase in radius increases the sinking rate for nonmotile cells that are denser than the surrounding water and decreases the minimum energy cost of motility per unit volume (Table 1). An increase in radius decreases the capacity of solute influx or efflux on a volume basis as a result of a thicker diffusion boundary layer and a smaller area of membrane lipid and number of transporters allowing, or catalyzing, solute fluxes (Table 1).

Most importantly for this article, an increase in cell radius decreases the average chl a -specific absorption coefficient (Table 1). This manifestation of the package effect (Kirk 1994) means that individual chl molecules have a lower probability of absorbing photons in a given radiation field in a large than a small unicellular organism, assuming a constant concentration of chl (mol per cubic meter of organism) and a constant spherical geometry. A correlate of the package effect is that the energy used to synthesize pigment-protein complexes takes longer to repay in terms of absorbed energy in a given external radiation field in larger cells (Raven 1984a). The package effect is also applicable to the effectiveness of intracellular UV-B screening compounds such as mycosporine-like amino acids, although quantitative analyses must take into account differences in the intracellular distribution of the photosyn-

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TABLE 1. Effect of cell size variation on the physical and physicochemical properties of spherical phytoplankton cells, assuming that cell composition per unit volume is independent of cell size.

Property	Effect of 10-fold increase of radius	References
Sinking speed (for cells denser than surrounding water)	Ten-fold increased speed (directly proportional to radius)	Raven (1986, 1999a,b)
Minimum energy cost of flagellar motility at a given speed	Ten-fold decrease in minimum energy cost of motility on a cell volume basis (directly proportional to radius)	Raven (1986)
Average chl <i>a</i> -specific absorption coefficient (lower value means more package effect, more intracellular self-shading)	Nonlinear decrease with increasing volume	Kirk (1994) Raven (1986, 1998, 1999a)
Average specific absorption coefficient for intracellular UV-absorbing compounds (lower value means more package effect, more intracellular self-shading)	Nonlinear decrease with increasing volume	Raven (1991, 1998, 1999a) Garcia-Pichel (1994)
Thickness of diffusion boundary layer restricting fluxes of solutes between cell surface and the bulk medium	Ten-fold increase in boundary layer thickness for radii less than $\sim 50 \mu\text{m}$; smaller increases in boundary layer thickness with radius increase at larger absolute radii	Raven (1986, 1998, 1999a,b) Ploug et al. (1999a,b)
Area of membrane per unit volume available for solute fluxes	Ten-fold decrease in membrane area per unit of volume	Raven (1986, 1998, 1999a,b)

thetic pigments and of the UV-B screening compounds (Raven 1991, 1998, 1999a, Garcia-Pichel 1994).

Some of these physical and physicochemical effects of increasing size also apply to some extent to small benthic algae. Clearly, sinking is not relevant here, although flagellar and gliding motility can occur in algal mats on mud on sand. Furthermore, boundary layer effects for organisms of small stature are overwhelmed by the diffusion boundary layer of the substratum. However, the "package effect" is as applicable to benthic as to planktonic algae (Raven 1999a,b).

Benthic algae can be of larger dimensions than planktonic algae. This is apparently at least in part as a result of evolutionary considerations of nutrient acquisition. Phytoplankton cells and organisms are never very large (up to a few millimetres in their maximum dimension; Raven 1986), probably related to diffusion boundary layer thickness around these organisms, which are only moving slowly (a millimeter per second or less) relative to their immediate surroundings (Raven 1986, 1994, Karp-Boss and Jumars 1998, Ploug et al. 1999a,b). Larger erect benthic algae have most of their thallus outside the substratum boundary layer, and the algal diffusion boundary layer can be minimized by water movements over the thallus (Raven 1999b). The large size of some erect benthic algae relates in part to competition for light (Raven 1999b). The larger dimensions of some benthic algae is not generally offset by a smaller concentration of photosynthetic pigments per unit volume, so that the optical thickness of the alga increases (Duarte et al. 1995, Raven 1999b). This greater optical thickness means that larger benthic algae have a large package effect so that the argument of Raven (1984a) regarding the decreasing energy benefit per unit energy cost for an increment in pigment concentration applies with even greater force than to smaller organisms.

In ontogeny the optical thickness of macroalgae generally increases as the organism increases in size.

This means that the juveniles of large erect macroalgae, which often grow in the shade of adult plants, have a smaller package effect than the adults. In terms of the energy benefit per unit energy cost for an increment of pigment concentration, a smaller optical thickness (and package effect) would to some extent offset the lower photon flux density incident on the juveniles (Raven 1999b, 2000). By contrast, adult macroalgae with a greater optical thickness and hence greater package effect are exposed to a higher photon flux density of PAR where the energy cost of synthesizing pigment-protein complexes is considered (Raven 1999b, 2000). Restricted light energy supply to juveniles can be offset in very early stages by larger parental investments in larger propagules, although many other considerations act on the natural selection of propagule size. Parental investment of resources may also be important in nitrogen and phosphorus supply because the juveniles are in the substratum diffusion boundary layer, which is thicker than that around adult erect portions of the alga (Raven 1999b). Of course, successful establishment of a benthic macroalgae from a propagule depends on a variety of abiotic and biotic factors (Vadas et al. 1992, Davison et al. 1993, Van Alstyne et al. 2001) in addition to energy supply.

In addition to the physical and physicochemical effects of size of algae, there are also biological effects of size. Very small algae are not accessible to certain phagotrophs that can only ingest larger food items, and vice versa. Furthermore, the smallest algae are probably inaccessible to eukaryotic parasites: there are insufficient resources in an alga or cyanobacterium with a volume equivalent to $1\text{-}\mu\text{m}$ spherical diameter to complete the life cycle of the parasite (Raven 1998, 1999a).

A further aspect of organism size is the extent to which resources can be stored. Defining storage in terms of the number of doublings of biomass that can

be supported by the endogenous reserves in the absence of further external supply, it is possible that larger organisms can have larger reserves than the very smallest organisms, which have little capacity to contain in their biomass anything but the essentials of metabolism (Raven 1998, 1999a). However, Raven (1984b, Tables 8.3 and 8.4) suggested that aquatic organisms can store an excess of N and P over the content that permits the maximum relative growth rate that permit two to three doublings regardless of organism size over a volume range of 10^{12} -fold, spanning nanoplankton and macrophytes.

These physical, physicochemical, and biotic factors can be used to predict what habitats the organisms of different size might occupy. These predictions are not uniformly in agreement with the observed distribution of the organisms (Chisholm 1992, Raven 1998, 1999a, Agawin et al. 2000a,b, Marañón et al. 2001); thus the deepest growing photolithotroph is a benthic alga with a relatively large package effect (Raven et al. 2000). However, some aspects of the occurrence of phytoplankton organisms of different sizes in particular habitat can be rationalized (e.g. picoplankton at deep chl maxima; Chisholm 1992, Raven 1998, 1999a,b, Moon-van der Staay et al. 2001).

DEPENDENCE OF RESOURCE-SATURATED SPECIFIC GROWTH RATE ON CELL SIZE

A correlate of the size of algae, and other organisms, is their growth rate. Larger algae have lower maximum specific growth rates at resource (light, nutrient) saturation than do smaller algae in the same phylogenetic group (see Raven 1999a,b). However, theoretical reasons (scalability of cellular components) and observations suggest that the increase in specific growth rate with decreasing cell size may not apply in the picoplankton size range (Raven 1998, 1999a,b, Dupuy et al. 2000). Although there are generally plausible models for size dependence of growth rate for larger organisms that have long-distance transport involving mass solution flow within the organisms (West et al. 1997), such models do not apply to smaller organisms (Beuchat 1997). By definition, these variations in specific growth rate are not a function of the supply of resources, because increasing resource supply does not increase specific growth rate.

The relationship between specific growth rate and organism size is expressed as

$$R = a \cdot W^{-b}$$

where R is the specific growth rate (e.g. mol C assimilated \cdot mol $^{-1}$ organism \cdot s $^{-1}$), W is a measure of the size of the organism (e.g. mol \cdot organism $^{-1}$), and a and b are constants (see Chisholm 1992). The value of a is often characteristic of a higher taxon, with significant difference between them; a is larger for diatoms than for dinoflagellates (Banse 1982, Chisholm 1992, Tang 1996). The value of b for resource-saturated growth is often taken as -0.25 (Finkel 2001), based on a very large body of data, but significantly lower (more negative) and, especially, higher values

are known for algae (Banse 1982, Chisholm 1992). To show the importance of these differences in the value of b for metabolic rates, a cell with 10^9 times the carbon content of a smaller cell has a specific growth rate $4.47 \cdot 10^{-2}$ that of the smaller cell if b is -0.15 , whereas the ratio of specific growth rates is $5.62 \cdot 10^{-3}$ if b is -0.25 and $7.08 \cdot 10^{-4}$ if b is -0.35 .

ORGANISM SIZE AND LIGHT-LIMITED SPECIFIC GROWTH RATES

For resource-limited growth and metabolism of algae there have been a number of predictions and measurements (Banse 1976, Schlesinger et al. 1981). Finkel and Irwin (2000) modeled algal photosynthetic rates under light-limiting conditions as a function of cell size. The prediction here is that larger cells with a given pigment content per unit biomass absorb less PAR per unit biomass in a given radiation field than do smaller cells as a result of the package (self-shading) effect (Finkel and Irwin 2000, see also Raven 1984a, Agustí 1991, Duarte et al. 1995). The outcome of the analysis is that the availability of excitation energy to individual photosynthetic reaction centers is less in larger than in smaller cells, assuming a constant photosynthetic pigment content per unit cell volume (Finkel and Irwin 2000).

The analysis of Finkel and Irwin (2000) shows, with constant photosynthetic pigment per unit volume and constant photosynthetic unit size, the exponent b of light-limited specific growth rate in Eq. 1 is more negative than -0.25 . Rates of photosynthesis at light saturation and at the growth photon flux density have values of b in Eq. 1 that are significantly lower (more negative) than -0.25 (Finkel 2001). This is in agreement with the model of Finkel and Irwin (2000) for photosynthesis under light-limiting conditions, taking into account the lower photosynthetic pigment per unit cell volume of larger diatom cells. To explain the low value of b for light-saturated photosynthesis, Finkel (2001) proposed an increase in the photosynthetic unit size (photosynthetic pigments per PSII reaction center) in larger cells with a larger package effect. However, it is not clear that there is sufficient functional variability in the size of the photosynthetic unit to account for the observed value of b . Another aspect of allometry in the work of Finkel (2001), which is not immediately explicable, is the low (less than -0.25) value of b for photosynthesis at both light saturation and at the (light-limiting) growth photon flux density, although the value of b for the light-limited specific growth rate and for the respiratory rate is -0.25 . The dependence of the light-limited specific growth on cell size cannot be predicted from the light-limited photosynthetic and the respiratory rates as a function of cell size. This discrepancy can be resolved if there is a significantly greater carbon-specific loss of organic carbon from smaller than from larger cells. Such a carbon-specific loss of organic carbon in smaller cells is as predicted from physicochemical considerations (Raven 1986), but further work is

needed to determine if there is such an allometry of organic carbon loss.

The recent studies of allometry of light harvesting provide important insights into the effects of cell size on phytoplankton physiology, but many questions remain. One such question concerns the effect of changes in the package effect as the size and shape of algae changes during the life cycle. Although a unicellular alga undergoing binary fission only changes in volume 2-fold over its asexual life cycle, a diatom undergoing vegetative size reduction can show change in mean cell volume 6-fold over months and an autospore alga can change in volume up to 16-fold over as little as 24 h under optimal growth conditions (van den Hoek et al. 1995, Graham and Wilcox 2000). Much greater changes in volume and shape, but smaller relative changes in optical thickness, occur in the ontogeny of macroalgae (Beach et al. 1995, Duarte et al. 1995, Raven 1999b). The greater rate of photosynthesis per unit photosynthetic pigment in a given radiation field in the earlier optically less dense stages in the ontogeny of macroalgae means that the younger stages, often growing in shaded habitats, have the potential for lower light compensation points than in the later more optically dense stages that may be in higher irradiances by virtue of their greater stature (see Raven et al. 2000).

The allometry of light harvesting also means that smaller optically less dense structures with a smaller package effect have a greater potential to use a larger spectral diversity of light-harvesting pigments than has a larger more optically dense structure (Dring 1981, Raven 1996, 1999a,b, 2000). The argument here is that the presence of a great spectral diversity of pigments in an optically dense structure has very little effect on the photon absorption rate, 400–700 nm, in a given radiation field relative to the same number of moles of pigment but with a smaller spectral diversity. By contrast, in smaller optically less dense structures, the smaller package effect means that each chromophore species behaves much more like it would in dilute monodisperse solution, so that additional spectrally diverse chromatophore species could cause more photon absorption over the 400- to 700-nm range in a given radiation field. Harvey (1836) pointed out that the colors of seaweeds could be better seen in propagules than in large thalli, a finding that can now be interpreted in terms of differences in optical thickness or density.

Allometry of light harvesting also has relevance to very short-term temporal variations in light supply. Phytoplankton cells in the picoplankton size range are rotated by very small-scale (Brownian) turbulence at rates similar to those (0.1–1 Hz, i.e. per second) at which (photosynthetically) constructive interactions of variations of photon flux density occur (Berg 1983, Mitchell 1991, Raven 1994). In a vector light field, and with a sufficient package effect, such rotation would cause potentially constructive variations in photon flux density incident on individual thylakoids

(Raven 1994). However, even with the highest possible concentration of photosynthetic pigment in the cells, the package effect is not very great in picoplankton cells, so the potential for stimulation is small (Raven 1994). More potential for such stimulation by rotation in a vector light field may occur in larger planktonic cells with, other things being equal, a greater package effect. Here the rotation by turbulence is too slow (<0.1 Hz), for nonspherical cells at least (Karp-Boss and Jumars 1998), to give photosynthetically constructive fluctuations in radiation intercepted by individual thylakoids, but the rotation at about 1 Hz during swimming of flagellates might cause constructive variations in incident photon flux density within the cell (Raven 1994, see Terry 1986). Further experimentation is needed to determine if the turbulence-driven rotation of very small phytoplankton (picoplankton) and rotation during swimming of flagellate phytoplankton cells interact via the package effect to give stimulation of photosynthesis through constructive variations in irradiance incident on thylakoids.

The arguments in Raven (1986) suggest that these rotation effects cannot be involved in the results of Finkel (2001) because the planktonic diatoms were too large for turbulence-driven rotation to occur at potentially constructive rates (Terry 1986), even if the experiments of Finkel (2001) had involved shaking of the cultures more frequently than once per day. However, theory suggests similar rotation rates for larger and smaller spherical cells, in a laminar shear field (Karp-Boss and Jumars 1998), at least for cells larger than picoplankton for which Brownian rotation is dominant (Mitchell 1991, Raven 1994). Rotation of larger optically dense cells of filaments *in situ* might then yield constructive interactions in photosynthesis (see Karp-Boss and Jumars 1998). Furthermore, the observed rotation speed of filaments of algal cells can exceed the computed rate; this may be important in nature but not in the work of Finkel (2001) (Karp-Boss and Jumars 1998). It is also of interest that the morphology of some motile dinoflagellate cells can be phenotypically determined by shear forces (Zirbel et al. 2000) and that the motion of swimming dinoflagellate cells in the presence of shear flow is not always predictable from the superposition of the flow on the swimming motion in absence of a flow (Karp-Boss et al. 2000). Vegetative cells of planktonic diatoms are, of course, nonmotile. There is scope for much more laboratory investigations of these effects of shear flow and for relating the results to natural variations in turbulence.

An extension of the effect of fluctuating light on growth rate of algae of different sizes and optical properties is the influence on competition among phytoplankton species (Litchman and Klausmeier 2001). The analyses (Litchman and Klausmeier 2001) of competition as a function of growth rate in fluctuating light for a species with a greater increment of specific growth per unit increase in incident photon

flux density in steady light but a lower specific growth rate at saturating steady light (*Sphaerocystis*) relative to a species with the opposite characteristics (*Nitzschia*) should be extended to include other than instantaneous transitions from growth rates at one photon flux density to that at the other photon flux density. As we see below, such nonlinear effects are particularly important at high frequencies of fluctuation (0.01–10 Hz).

For benthic macroalgae as a whole, the package effect is larger than in planktonic algae (Raven 1984a,b, Duarte et al. 1995). Short-term variations in light supply to the organisms as a whole are caused by such influences as waves altering refraction at the water surface and the configuration of overlying larger algae (Kübler and Raven 1999). The effects of these wave-frequency alterations in the photon flux density incident in *Ulva* are not always positive with respect to photosynthetic rates (Kübler and Raven 1999). The variations in the package effect with allometry, and with such regulatory events as plastid taxes that alter the position plastids within cells and hence their capacity for light interception in a given radiation field and thallus orientation, need further investigation in relation to changes in thallus conformation with water movement that can alter photon flux density arriving at thylakoids in the range of 0.1–1.0 Hz.

CONCLUSIONS

Quantitation of the influence of the package effect in algae of different sizes and shapes is clearly of importance in mechanistic interpretations of rates of photosynthesis and growth under natural conditions. Finkel (2001) and Finkel and Irwin (2000) have made a very significant contribution to this area of study, but much remains to be done. Potentially profitable areas of research include further study of the effects of fluctuations in light supply over the natural range of frequencies imposed by small-scale turbulence and vertical movement in the upper mixed layer for phytoplankton organisms and the effects of waves and currents for benthic algae as a function of organism size. Such studies should range from short-term studies of metabolism, growth, and competitive ability.

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