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Modeling Size-dependent Photosynthesis: Light Absorption and the Allometric Rule

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Microalgal photosynthesis can be predicted using empirical allometric or mechanistic bio-optic models. These two descriptions are usually considered independently. We compare the size scaling of photosynthesis predicted by these two models. Size scaling exponents for phytoplankton often deviate from the allometric 3/4 rule. This may be because the allometric model does not account for the size dependence of light absorption and its effect on the size scaling of photosynthesis. In contrast to the allometric model and experimental data, the bio-optic model predicts photosynthesis should be independent of cell size when intracellular pigment concentrations are low or inversely related to cell diameter. A composite of the allometric and bio-optic models is described and compared to laboratory data of light-limited nutrient-saturated diatom photosynthesis. The allo-bio-optic model provides a mechanistic explanation for the anomalous size scaling found in laboratory and field studies of microalgal photosynthesis and growth.

1. Introduction

An organism's size is a powerful predictor of its metabolic rates. The standard allometric model describes metabolic rate as a power law of organism size. Usually, the size scaling exponent associated with this relationship is 3/4 or when normalized to mass $-1/4$; this is referred to as the 3/4 rule. Phytoplankton make ideal experimental organisms for allometric studies, due to their extremely large size range. Phytoplankton include picoplankton which have diameters as small as 1 μm to netplankton that can reach diameters of close to a millimeter (Raven, 1994; Lin & Carpenter, 1995). Phytoplankton size is a good predictor of a variety of ecologically relevant rates. For example, size-dependent growth relationships reported in the literature have been used to estimate *in situ* rates of primary production from the size and taxonomic affiliation of the species making up the biomass profile (Joint & Pomroy, 1988; Joint, 1991). Although the allometric relationship can successfully model metabolic rates, anomalous size scaling exponents were used, and there is little information on how these exponents might change under different environmental conditions.

Several studies suggest that the metabolic rates of phytoplankton (growth, respiration and photosynthesis), while size-dependent have size scaling exponents significantly different from the commonly accepted 3/4 rule (Taguchi, 1976; Schlesinger *et al.*, 1981; Lewis, 1989; Tang, 1995). Furthermore, there is some evidence that different environmental conditions may affect the

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degree of size scaling (Banse, 1976; Schlesinger *et al*., 1981; Sommer, 1989). A recent study confirmed that light-limited centric marine diatoms have anomalously low size scaling exponents associated with their biomass-specific photosynthetic rate (Finkel, 2000). This leads to the suggestion that the size dependence of light absorption may modify the size scaling of anabolic rates. If this is the case, although the allometric model has been used to successfully describe the relationship between metabolic rate and cell size in heterotrophs from bacteria to large mammals, this model may be inadequate for photoautotrophs.

There are well-known mechanistic models which describe how light absorption and photosynthesis vary with cell size. Using a model of photosynthesis with changing light intensity, and a bio-optic model of light absorption by spherical phytoplankton cells, the role of light absorption in the size dependence of photosynthesis is examined and compared to the predictions provided by the allometric model. We combine the allometric and bio-optic models to examine how these two processes might interact and compare these predictions with results from laboratory and field studies.

2. Conceptual Framework

Three different models of the size dependence of photosynthesis are considered. First, a phenomenological allometric model, second a mechanistic bio-optic model, and finally a combination of the two which yields anomalous size scaling exponents. In all three cases photosynthesis is expressed as a function of incident light using a hyperbolic tangent function

$$P^* = P^*_{max} \tanh(\alpha^* I / P^*_{max}), \tag{1}$$

where the normalized photosynthetic rate, P^* is a function of incident irradiance, I, normalized photosynthetic capacity, P^*_{max}, and normalized photosynthetic efficiency, α^* (Jassby & Platt, 1976). Respiration is often subtracted from the right-hand side of eqn (1). Respiration often obeys the 3/4 rule, although some research suggests that respiration in algae may be anomalous, even independent of cell size (Lewis, 1989; Tang & Peters, 1995). Our goal is to focus on the effect of light absorption on the size dependence of photosynthesis and so we omit respiration from our analysis. Photosynthesis represents gross photosynthetic rate; the size scaling of growth may differ, depending on the size scaling of respiration. This paper considers only nutrient-saturated, light-limiting conditions. Under these conditions, maximum quantum yield is constant, and the impact of photosynthetic capacity is negligible, although this model of photosynthesis allows for the future examination of photosynthesis at any irradiance.

2.1. MODEL I: THE ALLOMETRIC MODEL OF PHOTOSYNTHESIS

Photosynthetic rate is related to cell size using the standard allometric model for metabolic rates:

$$\log P^* = m \log V + k, \tag{2}$$

where k is the intercept and m the slope of the relationship between the photosynthetic rate, P^* and the volume of the organism, V (Banse, 1976; Peters, 1983). Volume is used as a proxy for cell size but other measures such as carbon content can also be used. The intercept k is often quite variable (Fenchel, 1974; Chisholm, 1992). In contrast, regardless of the taxa considered, the slope m, often referred to as the size scaling exponent, is commonly $-1/4$ when the metabolic rate is normalized to body mass (Kleiber, 1961; Chisholm, 1992). The size scaling exponent is the same whether volume or carbon content is used as an indicator of cell size as long as carbon content per cell increases linearly with cell volume.

Using the commonly accepted empirical exponent of $-1/4$, the allometric model of normalized photosynthesis is

$$P^*_A = P^*_{A,max} \tanh(\alpha^*_A I / P^*_{A,max}) \approx \alpha^*_A I, \tag{3}$$

where

$$\alpha^*_A = k_{\alpha^*} V^{-1/4}, \tag{4}$$

$$P^*_{A,max} = k_{P^*_{max}} V^{-1/4} \tag{5}$$

and the proportionality constants k_{α^*} and $k_{P^*_{max}}$ are not of general interest. The photosynthetic function is approximated by $\alpha^*_A I$ since the photosynthetic response is approximately linear under low light intensities.

The size scaling of normalized photosynthetic capacity and efficiency are assumed to be $-1/4$, although we are aware that experimental results often deviate from $-1/4$. While the intercept of the allometric model is generally more variable it will have little effect on this analysis because it does not affect the size scaling of the metabolic rate. All model predictions reflect our interest in the relative, not absolute, magnitudes of the photosynthetic estimate with cell size.

2.2. MODEL II: THE BIO-OPTIC MODEL OF PHOTOSYNTHESIS

An alternative expression for photosynthetic rate is the product of the irradiance, the maximum quantum yield of photosynthesis (ϕ_{max}) and the absorption coefficient. The maximum quantum yield of photosynthesis is the number of moles of photons required to produce a mole of carbon product. The theoretical value of maximum quantum yield is 1/8, but a more realistic value is probably 1/10, which is used throughout (Kirk, 1994). At any given irradiance and quantum yield, the absorption coefficient determines photosynthetic rate.

Light absorption is a complicated nonlinear function of the pigment composition, concentration and cell size (Jassby & Platt, 1976; Morel & Bricaud, 1981; Kirk, 1994). Theory predicts absorption per unit of pigment becomes less effective as cells increase in size at a constant pigment concentration (Morel & Bricaud, 1981). This decrease in chlorophyll-specific absorption with increasing cell size or intracellular pigment concentrations is referred to as the package effect. Morel & Bricaud (1981) and Geider *et al.* (1986) describe the absorption coefficient as a function of the absorptive properties of the pigment–protein complexes, the concentration of the pigment within the cell, and cell size. The specific absorption coefficient of phytoplankton cells is given by

$$a^* = \frac{3}{2}\frac{a^*_s Q}{\rho}, \tag{6}$$

where

$$Q = 1 + 2\frac{e^{-\rho}}{\rho} + 2\frac{e^{-\rho} - 1}{\rho^2} \tag{7}$$

and

$$\rho = a^*_s c_i d, \tag{8}$$

where a^* has units of m^2 $(mg\,chl\text{-}a)^{-1}$, $a^*_s = 0.04\,(m^2\,(mg\,chl\text{-}a)^{-1})$ is the chlorophyll-specific absorption of the photosynthetic pigments in solution chosen to be within the range of values presented in Morel & Bricaud (1981), Q and ρ are dimensionless quantities, c_i (mg chl-$a\,m^{-3}$) is the intracellular chlorophyll-a concentration, and d is the cell diameter (m). The package effect can then be expressed as

$$\frac{a^*}{a^*_s}, \tag{9}$$

the ratio of the actual absorption of the pigments within the cell to the maximum absorption possible by the unpackaged photosynthetic pigments. When this ratio is small the package effect is large.

As in the allometric model, the bio-optic model assumes photosynthesis is a hyperbolic-tangent function of incident light, but the photosynthetic parameters are represented by different expressions. Photosynthetic efficiency is expressed as the product of ϕ_{max} and a, and the maximum photosynthetic capacity is

$$P^*_{B,max} = \frac{a^*\phi_{max}}{\sigma\tau} \tag{10}$$

where σ is the functional absorption cross-section of photosystem II, τ is the minimum turn-over time of the rate-limiting photosystem (Cullen, 1990; Falkowski & Raven, 1997). This treatment only considers sub-saturating light conditions where P^*_{max} is not achieved. Thus, the bio-optic model of photosynthesis can be expressed as

$$P^*_B = P^*_{B,max}\tanh(\alpha^*_B I / P^*_{B,max}) \approx \alpha^*_B I, \tag{11}$$

where $\alpha^*_B = a^*\phi_{max}$.

The bio-optic model provides a more detailed portrait of photosynthetic response than the allometric model. It can be used to examine photosynthetic rate for cells of an array of sizes and intracellular pigment concentrations. We consider cell volumes from 10^{-18} to $10^{-12}\,m^3$. Under a sub-saturating growth irradiance of $25\,\mu mol\,m^{-2}\,s^{-1}$ the bio-optic model, depending on the intracellular chlorophyll concentration, can predict a size scaling of photosynthesis similar to the predictions of the allometric model. Intracellular chlorophyll concentration has a strong effect on the size scaling of photosynthesis. Specific photosynthetic rate is shown for a number of different intracellular pigment concentrations in Fig. 1.

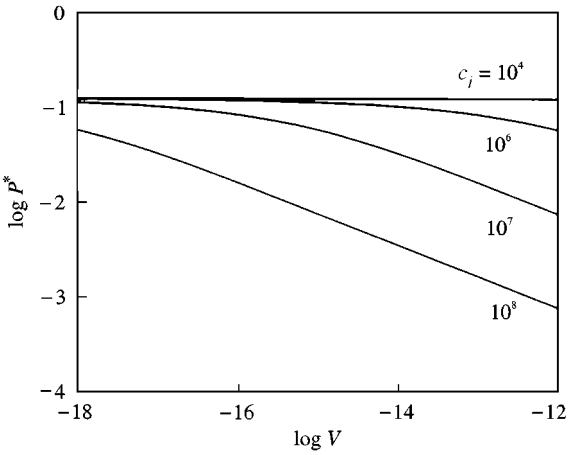

FIG. 1. Size-scaling of P^* as predicted by the bio-optic model. Each line represents a different intracellular chlorophyll-*a* concentration as labelled in the figure in units of m^{-2} mg chl-*a*. Volume is in m^3, and P^* is in mg C (mg chl-*a* h)$^{-1}$.

Models of photosynthetic rate can be used to generate mock experimental data, which can then be fit to an allometric model to obtain a size scaling exponent which might be obtained by an experimenter unaware of the underlying model. For the bio-optic model with intracellular chlorophyll concentrations from 10^4 to 10^9 mg chl-*a* m^{-3} (a very large range), this procedure gives exponents in the range of ~ 0 to -0.33. A size scaling exponent of ~ 0 occurs at very low intracellular pigment concentrations where all cells within the size range have no package effect. The size scaling exponent increases with intracellular pigment concentration. Cells of different sizes experience varying degrees of the package effect; small cells experiencing the least and large cells the greatest inefficiencies. Eventually, as the intracellular pigment concentration increases, all cells will experience an acute package effect. At this point the size scaling exponent becomes fixed at $-1/3$ (Fig. 1).

Experimental data indicate that intracellular pigment concentration varies inversely with cell diameter,

$$c_i \propto \frac{1}{d} \tag{12}$$

(Taguchi, 1976; Geider *et al.*, 1986; Agustí, 1991; Cullen *et al.*, 1993). If this relationship is added to the bio-optic model, both specific absorption and photosynthesis become independent of cell size, contrary to experimental data (Taguchi, 1976; Finkel, 2000). The following functional relationship has a similar shape with more flexibility, and avoids this difficulty:

$$c_i = \frac{k_3}{d + k_1} + k_2, \tag{13}$$

where k_1, k_2 and k_3 are constants to be determined from data. This allows for specific photosynthesis to increase with size under some conditions.

The bio-optic model also predicts that photosynthesis will become independent of size when c_i is low, as might be expected under high irradiance. Generally, the size scaling of metabolic rates measured under optimal environmental conditions suggest that although size scaling of algal growth may not correspond to $-1/4$, it does occur (Tang, 1995; Tang & Peters, 1995). The allometric model is able to predict photosynthesis and growth under these conditions, but depends on the determination of the anomalous size scaling exponent and does not incorporate the size scaling associated with absorptive processes. The shortcomings of these two models suggest a composite model may be better able to explain experimental data.

2.3. MODEL III: THE ALLO-BIO-OPTIC MODEL OF PHOTOSYNTHESIS

The allometric and bio-optic models can be combined to provide an estimate of the effect of both absorption and size scaled metabolism on the size scaling of phytoplankton photosynthesis. Unfortunately, it is difficult to determine how best to combine the allometric and bio-optic models due to the empirical nature of the allometric model. Two possible hybrid models are discussed below.

It seems logical to assume that the size scaling associated with light absorption is separate and independent from the size scaling of metabolic rates. This assumption is based on the existence of size scaling in the growth and respiratory processes of heterotrophs in the absence of light absorption. A hybrid model which combines the allometric scaling and bio-optic characteristics of photosynthetic efficiency has the following constraint. When the package effect is absent, e.g. at low intracellular pigment concentrations, the bio-optic effects should have no impact on the size scaling of photosynthetic efficiency. To reflect the independent nature of these two size scaling processes, the photosynthetic efficiency α_A associated with the allometric model and α_B associated with the bio-optic model are combined as a product

$$\alpha_{AB} = \alpha_A \alpha_B. \tag{14}$$

Allometric size scaling and the size scaling associated with light absorption is also assumed for P^*_{max}, although this is immaterial for the present analysis. The allo-bio-optic model is expressed as

$$P^*_{AB} = \alpha^*_{AB} I \tag{15}$$

$$\frac{\mathrm{d}\log P^*_{AB}}{\mathrm{d}\log V} = -\frac{1}{4} + \frac{\mathrm{d}\log P^*_B}{\mathrm{d}\log V}.$$

If α_B is independent of cell size this is unchanged from $-1/4$.

The allo-bio-optic model is more flexible than the allometric or bio-optic model alone. It predicts the size scaling of photosynthesis associated with both high and low intracellular pigment concentrations, and allows for the steeper size scaling one might expect if the allometric size scaling that occurs in heterotrophs also occurs in autotrophs (Fig. 2). Like the bio-optic model, the magnitude of the size scaling exponent increases (although it is substantially moderated) with c_i, from $\sim -1/4$ for low c_i (10^4 mg chl-a m^{-3}) to -0.58 for high c_i (10^9 mg chl-a m^{-3}) in the allo-bio-optic model. Unlike the bio-optic model, under low c_i, P^*_{AB} is size dependent with a size scaling exponent of $-1/4$. Similarly, when a realistic function for c_i is introduced [eqns (12) and (13)], photosynthesis remains size dependent with the standard size scaling exponent, or we obtain an exponent of -0.20, respectively. The empirical constants k_1, k_2 and k_3 were determined using data from Finkel (2000). If the constants are non-zero the size scaling of photosynthesis is affected. Compared to the standard size-scaling exponent of $-1/4$, the exponent decreases as k_1 increases above 0 and increases as k_1 decreases below zero; $-k_1$ represents the smallest cell diameter which can sensibly be described by eqn (13), approximately 1 μm (Fig. 3). The description of intracellular pigment concentration as a function of cell size affects the number of parameters in each model which affect the size scaling exponent. The allo-bio-optic model has 3–5 parameters depending on whether c_i is constant or eqn (12) or (13) is used. The allometric model has only one parameter (the size scaling exponent of $-1/4$) and the bio-optic model has

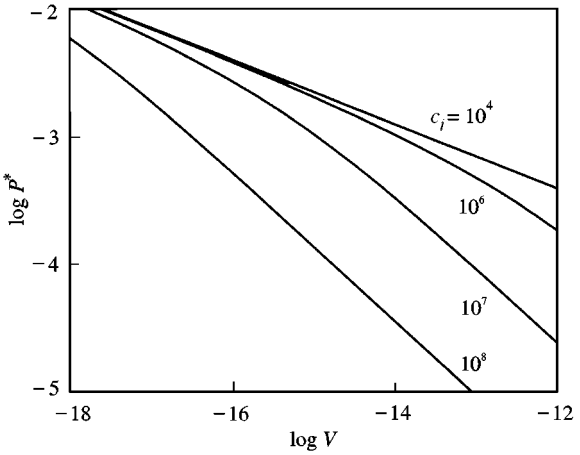

FIG. 2. Size scaling of P^* as predicted by the parallel allo-bio-optic model [eqn (15)]. Each line represents a different intracellular chlorophyll-a concentration as labelled in the figure. Units are the same as in Fig. 1.

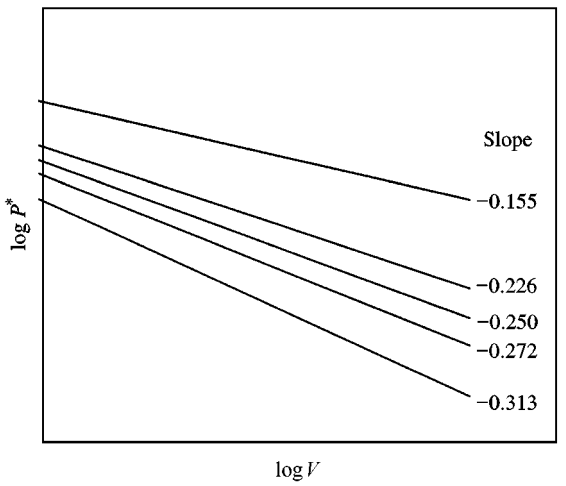

FIG. 3. Size scaling of P^* predicted by the parallel allo-bio-optic model as affected by the intracellular chlorophyll-*a* concentration. Intracellular chlorophyll-*a* concentrations are given by eqn (13). For each slope m the parameters are as follows: $m = -0.155$: $k_1 = -6 \times 10^{-7}$, $k_2 = 0$; $m = -0.226$: $k_1 = -4 \times 10^{-7}$, $k_2 = 0$; $m = -0.250$: $k_1 = 0$, $k_2 = 0$; $m = -0.272$: $k_1 = 7 \times 10^{-6}$, $k_2 = 0$; $m = -0.313$: $k_1 = 7 \times 10^{-6}$, $k_2 = 10^6$ with $k_3 = 24.69$.

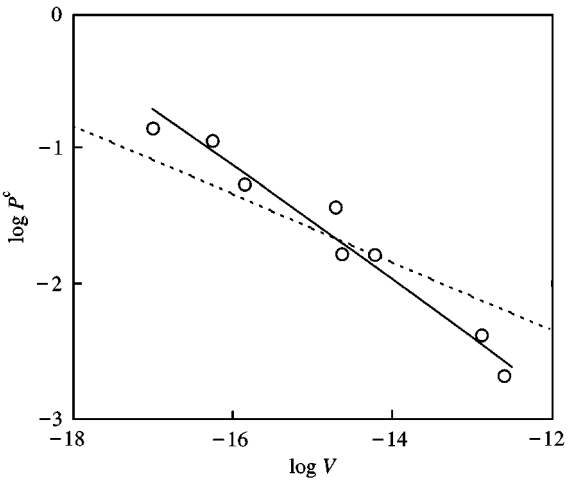

FIG. 4. A comparison of predictions of carbon-specific photosynthesis by the parallel allo-bio-optic model (solid line) and 3/4 allometric rule (dashed line) with experimental data (open circles) from Finkel (2000). Volume is in m^3, and P^C is in h^{-1}.

2–4 parameters (again, depending on the expression used for c_i). The allo-bio-optic model has more parameters, so we expect a better fit with data compared with the allometric or bio-optic models.

A direct comparison of the hybrid model and experimental data is shown in Fig. 4. Experimental photosynthetic rate (symbols) was calculated from average P^*_{max} and α^* using eqn (1) and converted to carbon-specific rates using the carbon-to-chlorophyll-*a* ratio using data from Finkel (2000). The allo-bio-optic model (solid line) uses parameters from the bio-optic model and a simplified version of eqn (13) with $k_1 = 0$, $k_2 = 273\,000$, and $k_3 = 1/27$ derived from experimental data (Finkel, 2000). A vertical translation was made to superimpose the theoretical curve on the data points. The agreement between the allo-bio-optic model and the data is qualitatively superior to the simple power law (dashed line): there is a shallower slope for small cells and the curve is concave down reflecting the changing package effect with increasing cell size. This provides convincing evidence that the anomalous size scaling of growth and photosynthetic rates could be due in part to the size dependence of light absorption.

The allo-bio-optic model above emphasizes the independence of the allometric and bio-optic processes with no sequential ordering. Another possible hybridization of the allometric and bio-optic models assumes the bio-optical processes occur before the allometric processes. The output of the bio-optical processes then provide the input for the allometric processes. Specific photosynthesis by the sequential allo-bio-optic model ($P^B_{AB'}$) is given by

$$P^*_{AB'} = \alpha^*_{AB'} I, \tag{16}$$

where

$$\alpha^*_{AB'} = k \left(\frac{a^*_s}{a^*} V \right)^m, \tag{17}$$

where a^*_s/a^* represents the consequences of the package effect on the input of energy into the subsequent allometric processes. This is an *ad hoc* description, and is just one possible way to incorporate the sequential nature of this effect.

The sequential allo-bio-optic model is shown in Fig. 5. Similar to the first hybrid model (the parallel model), the size scaling slope tends to $-1/4$ as c_i decreases and the package effect becomes negligible. As c_i increases, the size scaling exponent decreases to a minimum of $-1/3$ between 10^8 and 10^9 mg chl-*a* m^{-3}. Unlike the

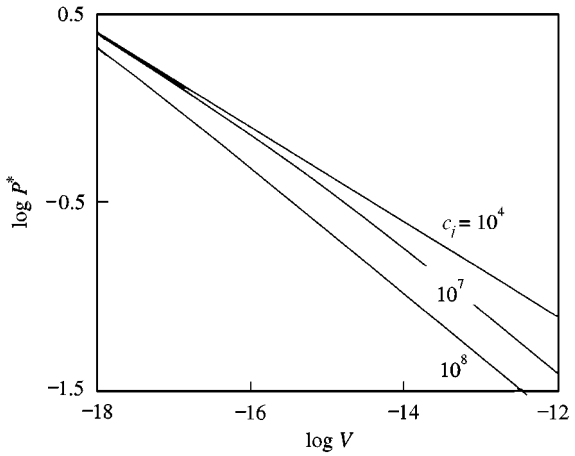

FIG. 5. Size scaling of P^* as predicted by the sequential allo-bio-optic model. Each line represents different intracellular chlorophyll-*a* concentration as labelled in the figure. Units are the same as in Fig. 1.

parallel model, the sequential model does not exhibit slopes steeper than $-1/3$ and the lines are much straighter over the range of cell sizes chosen. This is because the force of the package effect is reduced by the exponent $m = -1/4$ in eqn (17).

3. Discussion

We consider three kinds of models: allometric, bio-optic and allo-bio-optic models. Allometric models of growth and photosynthesis depend on the empirical relationship between metabolic rates and cell size. They are very simple models and are applicable to all taxa which makes them attractive tools. They provide good predictions of the metabolic rates of algae, but are inflexible and depend on the determination of the size scaling exponent under different environmental conditions and for different algal assemblages. Banse (1976) hypothesized that the size scaling of algal growth might decrease under sub-optimal growth conditions. Theoretical, field and laboratory data suggest that the size dependence of light absorption could affect the size dependence of anabolic rates (Schlesinger *et al.*, 1981; Finkel, 2000). This suggests that simple allometric models may not be good predictors of photosynthetic rate in unicellular algae.

Bio-optical models of photosynthesis depend on a mechanistic model of light absorption. This gives hope that photosynthesis can be predicted for a wide range of environmental conditions without performing new experiments for each situation. This would facilitate the estimation of primary production from satellite data. Unfortunately, the bio-optic model alone does not accurately describe the size scaling of photosynthesis under all conditions. When intracellular pigment concentration is low, the bio-optic model predicts that specific photosynthesis is independent of cell size, in contradiction with experimental data. As the intracellular pigment concentration increases, the bio-optic model predicts that size scaling will increase until a plateau is reached. This is because as intracellular pigment concentration increases, the package effect increases, decreasing photosynthesis. A number of studies suggest that intracellular pigment concentration varies inversely with cell diameter (Blasco *et al.*, 1982; Geider *et al.*, 1986; Agustí, 1991; Finkel, 2000). If $c_i \propto 1/d$ is introduced into the bio-optic model, photosynthesis becomes independent of size, again in contradiction with laboratory results and the allometric model. The bio-optic model is not always adequate to predict photosynthetic rates.

A combination of these two descriptions can improve predictions of photosynthesis and mimic anomalous size scaling seen in experimental data. This is achieved by incorporating the bio-optic properties of light absorption with the well-known phenomenological allometric description of phytoplankton metabolism. Specifically, the parallel allo-bio-optic model shows the same increase in magnitude of the size scaling exponent as found experimentally (Finkel, 2000).

The size scaling predicted by the bio-optic and allo-bio-optic models depend on the relationship between cell size and intracellular pigment concentration. Although chlorophyll-*a* is a common measure of biomass, the size dependence of c_i is often not reported. There is some evidence that suggests that the size dependence of c_i varies with environmental conditions and phylogenetic class. For example Chan (1978) found that diatoms tend to have higher chlorophyll-*a*-to-protein ratios than dinoflagellates. If dinoflagellates have lower intracellular pigment concentrations than diatoms of similar size, these dinoflagellates will have a smaller package effect, and the

allo-bio-optic model will predict a shallower size scaling exponent associated with dinoflagellate vs. diatom photosynthesis. The importance of the relationship between intracellular pigment concentration and the size scaling of photosynthesis is illustrated by eqn (13), in Fig. 3. The allometry of intracellular pigment concentration can explain both anomalously steep or shallow size scaling of photosynthesis. Similarly, the interrelationship between cell volume, carbon and pigment content is also of interest. Tang & Peters (1995) and Tang (1995) have demonstrated that the size scaling exponent will change when cellular carbon content is used instead of cell volume as a proxy of cell mass. This highlights the importance of understanding how cellular composition changes between species, between classes, under different environmental conditions and with cell size. Although there are many studies that have examined the cellular composition of phytoplankton, there is no obvious consensus on the relationship between cellular composition and cell size.

Several models of phytoplankton growth have been used to predict whether large or small cells should predominate under different environmental regimes (Parsons & Takahashi, 1973; Laws, 1975; Shuter, 1979; Schlesinger *et al*., 1981). Parsons & Takahashi (1973) predict that large cells are more likely to out-compete smaller cells under high light and nutrient-rich conditions. Laws (1975) and Shuter (1979) predict that large cells will only grow faster than small cells when light intensity is low. These models are fundamentally different from the allo-bio-optic models. Laws (1975) uses an allometric model of growth, where the anomalously steep size scaling of respiration favors the growth of large cells under certain environmental conditions. All the models use Michaelis–Menten-type nutrient kinetics, but each have a different description of the effect of light intensity on growth. Parsons & Takahashi (1973) describe light intensity like a nutrient, Laws (1975) use a photosynthetic efficiency-irradiance curve, and Shuter (1979) assumes carbon fixation is proportional to light intensity and the amount of carbon in the photosynthetic apparatus (which is affected by several environmental factors). None of these models use an explicit biophysical description of light absorption, or address the importance of the package effect. Factors such as the anomalous size scaling of respiration, and the description of how different light intensities and nutrient concentrations control growth rate alter the predicted cell size distribution for a given environmental condition.

The simple allometric model predicts that small cells should always out-compete large cells. The size dependence of photosynthesis in the bio-optic and allo-bio-optic models depend on the intracellular chlorophyll concentrations, so which sizes are most advantageous is not immediately clear. Our hybrid models show that the size dependence of light absorption can cause deviations from the standard size scaling exponents associated with photosynthesis in unicellular phytoplankton. The extent of the deviation depends on the interaction of metabolism and light absorption. Generally, it appears that if c_i is constant across the range of cell sizes, and of intermediate value, the size scaling exponent will be smaller than $-1/4$, but if c_i is low or varies inversely with cell size, light absorption will have little effect on the allometric size scaling. Future research should focus on the size dependence of c_i and how the predictions of the allo-bio-optic models might change under saturating irradiance and variable nutrient concentrations.

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