

REVIEW

Size dependence of growth and photosynthesis in diatoms: a synthesis

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ABSTRACT: The dependence of growth and photosynthesis on cell size in diatoms is evaluated in terms of an energy-balance model of microalgal physiology. Based on a review of available observations it appears that cell size can account for much of the interspecific variability in maximum growth rate (μ_m) and in optical absorption cross-section (a_{chl}). Both μ_m and a_{chl} decrease with increases in cell size. Cell size does not appear to influence the chlorophyll *a*:carbon ratio, the quantum efficiency of photosynthesis nor the photon flux density (PFD) at which growth rate is light-saturated. Available observations do not allow an evaluation of the size dependence of maintenance metabolic rates or the PFD at which light compensation of growth occurs. This analysis confirms the competitive advantage of small cell size of microalgae under nutrient-sufficient conditions at both light-saturating and light-limiting growth rates to the extent that small-celled diatoms have enhanced catalytic efficiencies of growth and light absorption.

INTRODUCTION

The unicellular algae range in size from cells of less than 1 μm diameter for some picoplanktonic chlorophytes and prasinophytes to cells of over 1 mm in length in some diatoms, dinoflagellates and chlorophytes (Sournia 1981). A number of selective pressures, some relating to the rates of energy use and nutrient transport by the cell, and hence to growth rate, and others relating to loss rates such as grazing and sinking, will be affected by cell size (Cavalier-Smith 1982).

Rates of metabolic processes in both multicellular and unicellular organisms generally have a size dependence that can be described by an allometric relation:

$$\text{rate} = aW^b \quad (1)$$

where 'rate' = the specific rate of some metabolic process (units of inverse time); W = a measure of

organism mass; a and b = coefficients (Peters 1983). When metabolic rates are expressed in units of inverse time and size is expressed in units of mass the exponent of the allometric relation generally takes values from -0.33 to -0.25 (Fenchel 1974, Banse 1982a, Peters 1983): in other words specific metabolic rates decrease with increasing size.

A reduction in cell division rate with increased size is documented in microalgae (Banse 1976, Blasco et al. 1982), although the magnitude of the exponent has been the subject of some discussion (Chan 1978, Banse 1982a). In particular, it appears that size dependence of metabolic rates only become statistically significant when organisms from a large range of sizes are considered and when care is taken to discriminate among metabolic and/or taxonomic types. For example, the growth rates of diatoms and dinoflagellates of equal size can differ by a factor of 3 and other groups appear to have intermediate growth rates (Banse 1982a). In addition to systematic variations in growth rates, different classes of microalgae are characterized by differences in chemical composition (Chan 1978, Hitchcock 1982).

Compounding the difficulty of making interspecific comparisons of growth and metabolic rates in microal-

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gae are the known phenotypic responses of chemical composition and metabolic rates to variations in environmental conditions. Phenotypic variations in intracellular pigment content, activities of various enzymes, photosynthesis and respiration rates, cell volume, and chemical composition occur in response to nutrient availability (Goldman 1980) photon flux density (Falkowski 1980) and temperature (Li 1980). This phenotypic variability should be taken into consideration when examining the size dependence of microalgal physiology.

A mechanistic model based on the flux of mass and energy through the algal cell can account for much of the phenotypic variability in microalgal physiology (Shuter 1979, Laws et al. 1983). Under nutrient-sufficient conditions this model reduces to an energy budget for microalgal growth (Laws et al. 1983, Geider 1984). Our investigation considers the size dependence of the variables in an energy budget for microalgal growth, but is limited primarily to the Bacillariophyceae because this is the class for which size effects on growth, photosynthesis and chemical composition are best documented. Information from other classes of microalgae and the cyanobacteria will be used where expedient or where useful comparisons can be drawn. Use of an energy budget facilitates the comparison of growth and metabolic rates with chemical composition and provides a means for organizing information from a number of different investigations into a unified treatment.

THEORETICAL MODEL OF MICROALGAL GROWTH

Recent theoretical models of microalgal growth (Shuter 1979, Kiefer & Mitchell 1983) have been based implicitly or explicitly on an account of the conservation of energy within a growing cell. Accounting for this energy budget is also an essential part of the empirical model of microalgal growth developed by Eppley & Sloan (1966) and Bannister's (1979) treatment of nutrient-saturated growth in *Chlorella*. Neglecting excretion, the energy balance simply states that the gross photosynthesis rate is equal to the sum of the growth and respiration rates (i.e. photosynthesis = growth + respiration). This section considers the parameterization of photosynthesis, growth and respiration rates in an energy budget equation. Later sections will consider the effects of cell size on the numerical values of the variables in the energy-balance equation. Symbols used in this paper are summarized in Table 1.

Following Kiefer & Mitchell (1983) one can express the photosynthesis rate as the product of a quantum efficiency of photosynthesis, an absorption cross-section

Table 1. Summary of notation. All symbols are defined on first appearance in the text; commonly occurring symbols are summarized here for convenience

Symbol	Definition
I	Photon flux density
P ^c	Carbon-specific photosynthesis rate
P _m ^c	Carbon-specific, light-saturated photosynthesis rate
P _m ^{chl}	Chlorophyll <i>a</i> -specific, light-saturated photosynthesis rate
Z	Dimensional constant equal to the atomic mass of carbon
a _{chl}	Chlorophyll <i>a</i> -specific, light absorption coefficient
r	Respiration rate
r _m	Maintenance metabolic rate
α	Initial slope of the photosynthesis-light response curve
φ _p	Photon (quantum) efficiency of gross photosynthesis
φ _m	Maximum photon efficiency of photosynthesis
θ	Chlorophyll <i>a</i> : carbon ratio
μ	Growth rate
μ _m	Maximum, species-specific growth rate
ξ	Energy cost of synthesis

tion expressed on a unit chlorophyll *a* basis, the cell chlorophyll *a*:carbon ratio and the photon flux density (PFD):

$$P^c(I) = Z \varphi_p a_{chl} \theta I \quad (2)$$

where $P^c(I)$ = gross photosynthesis rate in units s^{-1} ; Z = a dimensional constant equal to the atomic mass of carbon (0.012 mgC/ μ mol C); φ_p = the quantum efficiency of photosynthesis (mol C/mol photons); a_{chl} = the chlorophyll *a*-specific absorption cross-section ($m^2/mg\ chl a$); θ = the chlorophyll *a*:carbon ratio (mg chl *a*/mgC); I = the photon flux density (μ mol photons $m^{-2} s^{-1}$).

This treatment differs from Shuter (1979) by considering the quantum efficiency and absorption cross-section separately whereas Shuter considers only the product of the 2 terms. Also, unlike Shuter, we do not consider the product ($\varphi_p a_{chl}$) to be constant.

Kiefer & Mitchell (1983) considered the quantum efficiency of photosynthesis to decrease with increases in PFD:

$$\varphi_p = \varphi_m K / (K + I) \quad (3)$$

where K = a coefficient that characterizes the decrease of efficiency of photosynthesis with increases in PFD; φ_m = the maximum quantum efficiency of photosynthesis. It can be shown that the PFD dependence of φ_p implied by Eq. 2 & 3 implies a rectangular hyperbolic

expression for the photosynthesis-light curve (Laws et al. 1985) which is but one possible 2-parameter equation for the PI curve. For PFDs which are not photo-inhibitory the light dependence of gross photosynthesis can be described using several 2-parameter equations (Jassby & Platt 1976). In this discussion we assume that the rate of photosynthesis can be described using an exponential function (Eq. 4), although other saturating functions, such as the rectangular hyperbola, can be employed.

$$P^{\text{chl}}(I) = P_m^{\text{chl}} [1 - \exp(\alpha I / P_m^{\text{chl}})] \quad (4)$$

where $P^{\text{chl}}(I)$ = the chlorophyll *a*-specific gross photosynthesis rate ($\text{mg C} [\text{mg chl}a]^{-1} \text{s}^{-1}$); P_m^{chl} = the light saturated, chlorophyll *a*-specific gross photosynthetic rate; α = the initial slope of the PI curve with units of $(\text{m}^2/\text{mg chl}a) (\text{mg C}/\mu\text{mol photon})$.

The initial slope can be expressed as the product of the absorption cross-section, the maximum quantum efficiency of photosynthesis and a dimensional constant (Eq. 5), and the chlorophyll *a*-specific light saturated photosynthesis rate can be expressed as a function of the chlorophyll *a*:carbon ratio and a carbon-specific, light-saturated photosynthesis rate (Eq. 6):

$$\alpha = \varphi_m a_{\text{chl}} Z \quad (5)$$

$$P_m^{\text{chl}} = P_m^{\text{c}} / \theta \quad (6)$$

where P_m^{c} = the carbon specific, light-saturated photosynthesis rate (s^{-1}); the other terms are as defined above.

The actual quantum efficiency of photosynthesis (φ_p), as distinguished from the maximum quantum efficiency (φ_m), can be expressed in terms of the parameters of the PI curve as follows

$$\varphi_p = \varphi_m [P^{\text{chl}}(I) / \alpha I] \quad (7)$$

Substituting Eq. 4 into 5 followed by 5 and 6 into 7 yields

$$\varphi_p = P_m^{\text{c}} [1 - \exp(Z \varphi_m \theta I / P_m^{\text{c}})] \quad (8)$$

Eq. 8 illustrates that the quantum efficiency of photosynthesis is not independent of the other variables in the PI curve (i.e. φ_m , a_{chl} , θ , P_m^{c}). In this respect our treatment differs from Kiefer & Mitchell (1983) who consider φ_p to depend on PFD through Eq. 3 and the parameter K . It is not clear from Kiefer & Mitchell's (1983) analysis to what extent the decline in φ_p is due to a decrease in the initial slope of the PI curve or a decrease in photosynthesis rate due to light saturation.

Substituting the expression for the quantum effi-

ciency of photosynthesis (φ_p as given in Eq. 8) into Eq. 2 yields

$$P^{\text{c}}(I) = P_m^{\text{c}} [1 - \exp(Z \varphi_m a_{\text{chl}} \theta I / P_m^{\text{c}})] \quad (9)$$

Eq. 9 and Eq. 2 & 3 are alternative expressions of the photosynthesis-light curve written in terms of the same parameters. Our treatment differs from Kiefer & Mitchell (1983) in that Eq. 9 is a PI curve based on an exponential function whereas Eq. 2 & 3 yield a PI curve based on the rectangular hyperbola. This in itself is a trivial difference related only to the mathematical function chosen to describe the shape of the PI curve. In Eq. 9, however, the entire PI curve is explicitly considered, whereas Eq. 2 & 3 refer only to the rate of photosynthesis at a single PFD (i.e. the light level to which the cells are acclimated). The consideration of the entire PI curve results from the introduction of an additional and potentially useful photoadaptive variable (i.e. the light-saturated photosynthesis rate P_m^{c}).

The other components of the energy budget for growth are the growth rate and the respiration rate. Following Shuter (1979) the respiration rate can be expressed as the sum of a maintenance metabolic rate and a growth-rate-dependent cost of cell synthesis, where again the rates are expressed in units of inverse time:

$$r = r_m + \mu \xi \quad (10)$$

where r = the respiration rate (s^{-1}); r_m = the maintenance metabolic requirement (s^{-1}); μ = the growth rate (s^{-1}); ξ = the cost of synthesis (dimensionless).

The energy balance equation [photosynthesis = growth + respiration] can be written as follows:

$$\mu(1 + \xi) + r_m = P_m^{\text{c}} [1 - \exp(Z \varphi_m a_{\text{chl}} \theta I / P_m^{\text{c}})] \quad (11)$$

This model contains 1 independent environmental variable (I), and 7 dependent metabolic variables (μ , r_m , ξ , θ , φ_m , a_{chl} , and P_m^{c}). We will refer to a variable as photoadaptive if its numerical value depends on PFD at which a microalga is growing.

The remainder of this paper considers the size dependence of microalgal metabolism in terms of the size dependence of the variables in the energy balance equation (Eq. 11). In this way information derived from a number of independent sources can be combined in a unified treatment of nutrient-sufficient microalgal metabolism.

Maintenance metabolic rate (r_m)

Processes which contribute to the maintenance metabolic costs include the turnover of the macro-

molecular components of the plant cell and the maintenance of solute gradients between the cell and its environment (Raven 1976). The numerical value of the maintenance metabolic rate is usually considered to be independent of growth rate, but dependent on cell mass in bacteria and microalgae (Pirt 1965, Shuter 1979). The flux of solutes into or out of the cell should be proportional to cell surface area (Raven 1984a), and the mass-specific cost of solute regulation should thus depend on the relation (Strathman 1967) between cell mass and cell volume. In contrast, the mass-specific maintenance cost (units of inverse time) for turnover of the macromolecular components of a cell should be independent of cell mass.

The numerical value of maintenance metabolic rate has been estimated from extrapolation of growth-rate-dependent, dark respiration rates to zero growth (Laws et al. 1983, 1985), measurement of respiration rates after prolonged (several hour) incubations in darkness (French et al. 1934), or extrapolation of light-limited growth rates to zero growth (Van Liere & Mur 1979). The limited number of observations preclude an empirical evaluation of the size dependence of r_m . We will use a constant value of $r_m = 0.7 \times 10^{-7} \text{s}^{-1}$ based on observations for marine microalgae (Laws & Caperon 1976, Laws & Wong 1978, Verity 1982). Estimates of r_m for freshwater chlorophytes are somewhat larger (2 to $3.5 \times 10^{-7} \text{s}^{-1}$) based on the summary in Van Liere & Mur (1979).

Energy cost of synthesis (ξ)

The cost of synthesis accounts for the energy required for production of the complex macromolecules which make up the algal cell from simple carbohydrates (considered to be the initial products of photosynthesis) and inorganic nutrients. The cost of synthesis can be calculated from a consideration of the biochemical pathways leading to the synthesis of the major classes of macromolecules (protein, lipid, nucleic acids, carbohydrates) including the costs of assimilating inorganic ions (Penning de Vries et al. 1974, Raven 1976). As a consequence ξ should vary with the form of the inorganic nutrients used for growth, especially with respect to the form of nitrogen supplied, and the chemical composition of the microalgae as reflected in the carbon:nitrogen ratio (for example see Shuter [1979]).

Direct estimates of ξ have been based on the slopes of linear regressions of mass-specific dark respiration rate (r_d) on growth rate (Laws et al. 1983). The slopes of these regressions (Laws & Caperon 1976, Laws & Wong 1978, Verity 1982, Laws et al. 1983) generally yield values of ξ which are less than those derived from

theoretical analyses described in the preceding paragraph, and r_d is independent of growth rate in several species examined (Falkowski et al. 1985, Geider et al. 1985). It appears that the r_d is not a good indicator of metabolic processes occurring in the light (Raven 1976), and that we must rely on theoretical calculations (Penning de Vries et al. 1974, Raven 1976) for an evaluation of the energy costs of synthesis. For this discussion we will consider ξ to have a fixed value that can, however, depend on the inorganic nitrogen source.

Maximum quantum efficiency of photosynthesis (φ_m)

The maximum quantum efficiency of photosynthesis (φ_m) is constrained by the Z scheme of photosynthesis to a value of less than 0.125 mol O_2 /mol photons. There is a substantial energetic inefficiency even in this maximum attainable value, because of the requirement that the transformation of energy from photons to chemical bonds proceeds unidirectionally and at a finite rate (Raven 1984a). In practice, somewhat lower efficiencies would be expected due to energy losses from back reactions at the reaction centers, inefficiencies of energy transfer in antennae pigments and multiple hits on closed reaction centers (Myers 1980). A commonly accepted value for φ_m is 0.10 mol O_2 /mol photons (Senger 1982). The maximum quantum efficiency does not appear to depend on the light level to which a species is acclimated (Senger & Fleischhacker 1978, Ley & Mauzerall 1982, Geider et al. 1985), and there is little evidence to suggest interspecific variations. For these reasons we will consider φ_m to be constant, although we recognize that the magnitude of φ_m is still contentious (Pirt 1983). Implicit in Eq. 11 is a photosynthetic quotient of unity.

Light-saturated, carbon-specific photosynthesis rate (P_m^c)

There are relatively few observations of the dependence of P_m^c on the light level to which cells have been acclimated. Mass-specific and carbon-specific, light-saturated photosynthesis rates show less than 2-fold variations over a wide range of PFDs in nutrient-sufficient cultures of several species of microalgae (Myers 1970, Prézelin 1976, Foy & Gibson 1982, Vincent 1982, Chang et al. 1983, Raps et al. 1983, Geider 1984, Geider et al. 1985). For this discussion we assume that P_m^c is a species-specific constant. This is similar to the approach taken by Steele (1962) in an interesting discussion of environmental control of photosynthesis and the chlorophylla:carbon ratio in the sea. There is insufficient data to evaluate the size dependence of P_m^c .

bers of chloroplasts in microalgal cells and other cytological changes which would take place in the cyanobacteria. Observations of a_{chl} , θ , and cell carbon for *Thalassiosira weissflogii*, *Isochrysis galbana* and *Procentrum micans* (Falkowski et al. 1985) are consis-

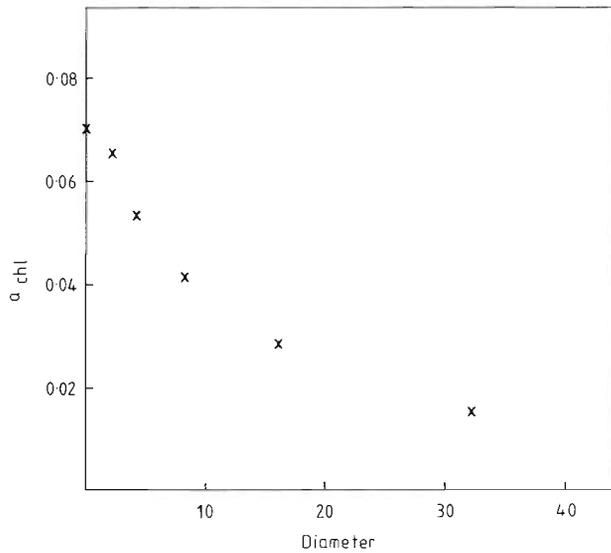


Fig. 2. Dependence of chlorophyll *a*-specific absorption cross-section (435 nm) on cell diameter as predicted by MIE theory for spherical, homogeneous cells (data from tabular summary of Morel & Bricaud 1981). Units for a_{chl} and cell diameter are, respectively, $m^2/mg\ chl\ a$ and μm

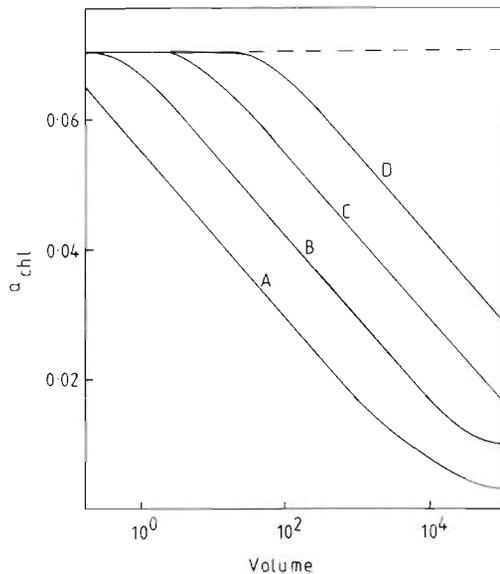


Fig. 3. Dependence of chlorophyll *a*-specific absorption cross-section on cell volume (μm^3) and chlorophyll *a*: carbon ratio for homogeneous, spherical cells as predicted by MIE theory. Different values for the chlorophyll *a*:carbon ratio are indicated as follows: A, 0.067; B, 0.033; C, 0.017; D, 0.0083 g chlorophyll *a*/g carbon. Note that the observations from Fig. 2 are represented by line B of this figure

tent with reduction of a_{chl} in highly pigmented or large cells as illustrated in Fig. 4. In Fig. 4 a_{chl} is plotted against the product $(\theta C^{0.33})$ which is a measure of the dimensionless parameter q . The cube root of cell carbon content is used as a measure of cell diameter and the chlorophyll *a*: carbon ratio is a measure of intracellular pigment content.

Indirect evidence for a reduction of a_{chl} with increases of cell size is provided by the observed reduction of the initial slope (α) of the PI curve (Taguchi 1976; Fig. 5) in large cells, which for a constant maximum quantum efficiency (ϕ_m) of photosynthesis implies variable a_{chl} (see Eq. 5).

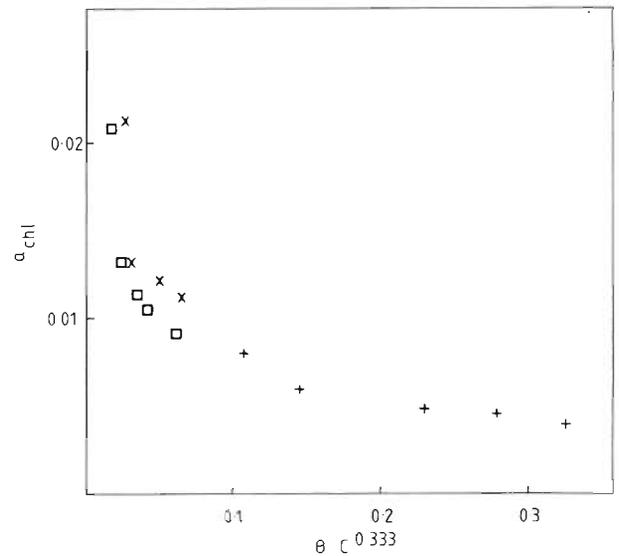


Fig. 4. Observed dependence of chlorophyll *a*-specific absorption cross-section on cell carbon content (C) and chlorophyll *a*: carbon ratio (θ) in 3 species of marine microalgae: (\square) *Isochrysis galbana*; (+) *Thalassiosira weissflogii*; (\times) *Procentrum micans*; observations are from Falkowski et al. (1985). Absorption cross-section (a_{chl}) is plotted against the product $(\theta C_{0.33})$. Note the similarity of the shape of the curve to MIE theory predictions illustrated in Fig. 2

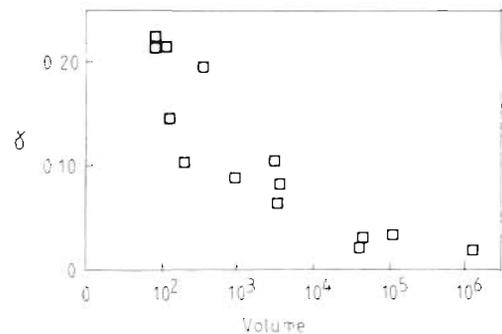


Fig. 5. Relation between initial slope of the photosynthesis-light curve and cell volume in marine diatoms. Observations are from Taguchi (1976). Initial slope has units of $(mg\ C) (mg\ chl\ a)^{-1} h^{-1} W^{-1} m^2$ and cell volume has units of μm^3

Light curve of growth

Growth rate is a saturating function of PFD at low to intermediate PFDs before the onset of photoinhibition at high light levels. To describe the light curve for growth (μ -I curve) requires the specification of at least 3 parameters. These are the light-saturated maximum growth rate (μ_m), the compensation PFD (I_c), and a parameter that describes the PFD at which growth rate becomes light saturated (I_k).

The maximum growth rate of diatoms ranges from about 3 d^{-1} ($3.5 \times 10^{-5} \text{ s}^{-1}$) for cells of under $100 \mu\text{m}^3$ volume to under 1 d^{-1} ($1.1 \times 10^{-5} \text{ s}^{-1}$) for cells of about $10^6 \mu\text{m}^3$ volume at about 20°C (Banse 1982a, Blasco et al. 1982). The size dependence of nutrient-sufficient maximum growth rates is well documented in the diatoms (Fig. 6) and can be described by an allometric relation:

$$\mu_m = a W^b \quad (16)$$

The slope of regressions of $\log(\mu_m)$ on \log cell mass yields an exponent which is greater than -0.25 , the expected value if metabolic rates are scaled with cell mass as in most heterotrophs (Banse 1982a); for example, Blasco et al. (1982) give a value of $b = -0.14$ for growth and $b = -0.125$ for carbon-specific ^{14}C uptake rates in diatoms.

The minimum light level which supports growth of diatoms was found by Richardson et al. (1983) to be $6.4 \pm 0.9 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (mean ± 1 standard error), which is probably an overestimate of the compensation PFD (I_c) because of the limitations of the data

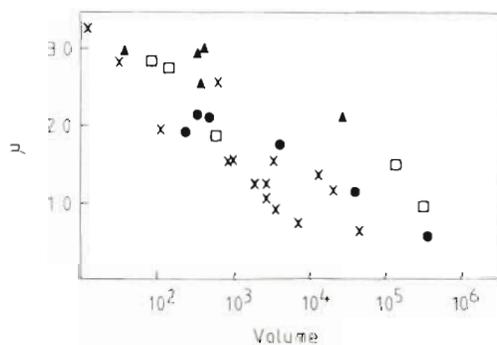


Fig. 6. Size dependence of nutrient-sufficient growth rates (μ) in diatoms. Each symbol represents a set of observations taken from a single investigation in which conditions of temperature and photon flux density were held constant; (\times) Williams (1964); (\square) Blasco et al. (1982); (\blacktriangle) Chan (1978); (\bullet) Eppley & Sloan (1966). Excluded are observations for *Cosinodiscus* sp. CoA(14) from Blasco et al. which lies off the right hand margin and observations for *Cosinodiscus asteromphilus* and *Thalassiosira fluviatilis* growing at 20°C from Eppley & Sloan. Growth rate is expressed in units of d^{-1} and volume is expressed in units of μm^3

base of growth measurements at low PFDs. For example, several species of diatoms for which detailed μ -I curves are available at low PFDs yield values of I_c of under $1 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (*Thalassiosira pseudonana* and *Phaeodactylum tricornerutum*, Nelson et al. 1978; *Skeletonema costatum*, Falkowski & Owens 1980). It is unfortunate that there are few observations of the light dependence of microalgal growth which extend to extremely light-limited conditions (i.e. light-limited growth rates of under 20 % of the light-saturated rate). At present there are too few observations of light-limited diatom growth to determine if there is a size dependence of the compensation PFD.

The PFD at which growth rate of diatoms becomes light saturated (I_k) was found to be 84 ± 8.1 (mean \pm standard error) $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Richardson et al. 1983). The value of I_k is better constrained by experimental observations than the value of I_c because most observations of the light dependence of growth include saturating and somewhat subsaturating PFDs. Of particular interest for this discussion is the low ratio of standard error to mean which indicates little interspecific variation in the light requirements for growth within the diatoms. Where observations of the μ -I curve are available for more than 1 species or clone under the same experimental conditions (Chan 1978, Nelson et al. 1978, Terry et al. 1983) plots of relative growth rate (μ/μ_m) against PFD show only minor differences. Although occasionally of poor resolution, these observations indicate that most species of diatoms can be characterized by the same value of I_k independent of cell size.

DISCUSSION

Of the variables in an energy balance for microalgal growth described in the preceding section, one can tentatively conclude that the maximum quantum efficiency of photosynthesis (ϕ_m), the energy cost of synthesis (ξ) and the chlorophyll *a*:carbon ratio (θ) are independent of cell size, whereas the chlorophyll *a*-specific absorption coefficient (a_{chl}) and the maximum growth rate (μ_m) decrease with increases in cell size. There is insufficient experimental evidence to evaluate the size dependence of the maintenance metabolic rate (r_m), which in any case is a small fraction of μ_m and will only become a significant determinant of the growth rate at low PFDs.

The maximum growth rate can be considered as a carbon-specific catalytic activity (i.e. as the flux of carbon per unit cell carbon; $[1/C] [dC/dt]$), and since chlorophyll *a* is a major photosynthetic light-harvesting pigment of diatoms, a_{chl} can be considered as a pigment-specific light-harvesting efficiency. There is a theoretical basis for a reduction of a_{chl} with increased

cell size because of self-shading of pigments in large cells which contain the same chlorophyll *a*:carbon ratio as smaller cells (Morel & Bricaud 1981, Raven 1984b). A theoretical basis for reduction of μ_m with increased microalgal cell size is more elusive. Large microalgae have the same basic intracellular compartmentation as small cells, so increased complexity cannot be invoked as a determinant of μ_m . In addition, it has been suggested that the proportion of cell mass invested in non-catalytic, structural material decreases with increased cell size (Shuter 1979) and so a higher μ_m might be anticipated in larger cells.

Banse (1982a) has recently noted that the size dependence of μ_m in microalgae is less pronounced than in heterotrophs, and on the basis of scatter in the available observations of μ_m and size in diatoms and dinoflagellates concluded that the size dependence of μ_m was undecided. In heterotrophs maximum specific growth rate (units of inverse time) scales with $\text{mass}^{-0.275}$ (Fenchel 1974) whereas recent observations of Blasco et al. (1982) indicate a $\text{mass}^{-0.14}$ dependence of μ_m for diatoms.

To derive a general expression for the light-curve of growth from a consideration of the dependence of the variables in the energy balance equation on cell size and PFD will not be a simple exercise primarily because of the dependence of θ on PFD, and through θ the PFD dependence of a_{chl} . However, we can consider the particular cases of light-limited and light-saturated growth separately to gain some insights into the interrelations among the variables in the energy balance model (Eq. 11). At low PFDs which are within the linear region of the PI curve the energy balance reduces to the following:

$$\mu = [(Z a_{chl} \varphi_m \theta I) - r_m] / (1 + \xi) \quad (17)$$

For a constant value of θ at any particular PFD (Fig. 1), the reduction in a_{chl} with increased cell size will result in a reduced light-limited growth rate in larger cells. Thus, the initial light-limited slope of the light curve for growth should decrease with increases in cell size. A reduction in r_m with increased cell size could potentially counterbalance this effect; however, given the low observed values for r_m , such a reduction would be of limited extent.

There is some indirect evidence for the predicted reduction of the initial slope of the μ -I curve. Observations of Williams (1964) for nutrient-sufficient growth at a light level that is likely to be non-saturating for growth yields a size dependence which is greater than the size dependence of μ_m reported elsewhere (Banse 1982b). However, Banse (1982b) has noted limitations of the Williams (1964) data set, in particular with regard to the limited number of observations used for

growth rate calculations. Observations of Schlesinger et al. (1981) indicate that the size dependence of growth rate is more pronounced at high (12 W m^{-2}) than at low (2 W m^{-2}) light levels, although all of these light levels are likely to be within the initial, linear portion of the light curve for growth.

Eq. 17 can be used to evaluate the compensation light level (I_c) for growth by setting $\mu = 0$, and solving for $I = I_c$:

$$I_c = r_m / (Z a_{chl} \varphi_m \theta) \quad (18)$$

Given a reduction in a_{chl} with increased cell size and assuming r_m is independent of size, Eq. 18 indicates that I_c should be larger in big cells than in small cells. To the best of our knowledge, there is no evidence available which can be used to directly test this hypothesis. In particular, there are few observations of microalgal growth at PFDs near the compensation PFD.

Under conditions in which both the photosynthesis rate and the growth rate are light-saturated the energy balance equation reduces to the following:

$$P_m^c = \mu_m (1 + \xi) + r_m \quad (19)$$

Noting that r_m will typically be less than 5 to 10% of μ_m , Eq. 19 indicates that light-saturated, carbon-specific growth rates should be proportional to light-saturated, maximum photosynthesis rates. To the best of our knowledge, this hypothesis is not verifiable with the available data on growth and the PI curve in microalgae.

Substituting $P_m^c = [\mu_m(1 + \xi)]$ into the energy balance equation, neglecting r_m which is small relative to μ at all but the lowest light levels, and substituting $[\mu' = \mu/\mu_m]$ where μ' is the relative growth rate leads to:

$$\mu' = \mu_m (1 + \xi) \{1 - \exp [Z a_{chl} \varphi_m \theta I] / [\mu_m (1 + \xi)]\} \quad (20)$$

The conclusion of Richardson et al. (1983) that the light curve of growth for different diatom species appears to saturate within a narrow range of PFDs constrains the relation among the variables in the exponential function of Eq. 20. In particular, it is required that the product of the variables will be independent of size. We have already noted that a_{chl} and μ_m are the only variables which are size dependent, a conclusion based on the independent investigations reviewed in the preceding sections (Fig. 3, 4 & 5). It follows from Eq. 20 and the observation that growth saturates at similar PFDs in most diatoms that μ_m and a_{chl} have essentially the same size dependency. This

implies covariance of a_{chl} and μ_m , and because of the suggested relation of P_m^c and μ_m this also implies covariance of a_{chl} and P_m^c . The observed correlation of the initial slope and light-saturated rate of the PI curve in samples of natural phytoplankton (Platt & Jassby 1976) may reflect similarities in the size dependence of these variables, although other explanations have been advanced (Harris 1978). Also consistent with this hypothesis is the observation that oceanic picoplankton ($< 1 \mu\text{m}$ diameter) are characterized by higher initial slopes ($\alpha = \varphi_m a_{chl}$) and light-saturated photosynthesis rates (P_m^{chl}) than larger ($> 1 \mu\text{m}$ diameter) phytoplankters (Platt et al. 1983), although possible taxonomic differences between organisms in different size fractions (Furnas 1983) should not be ignored.

The reduction of μ_m and a_{chl} with size implies that small cells have a distinct catalytic advantage over large cells and should outcompete large cells at both high and low light levels. Observations of nutrient uptake by natural phytoplankton populations (Friebele et al. 1978, Smith & Kalf 1982), of kinetic parameters of nutrient uptake in unialgal cultures (Malone 1980b citing Eppley et al. 1969 and Carpenter et al. 1971) and competition experiments in chemostat cultures (Turpin & Harrison 1980) indicate that small-celled species are more efficient nutrient scavengers than large-celled algae. Finally, the sinking rate of phytoplankton generally increases with increased cell size (Smayda 1970, Eppley 1977) reducing the residence time of large-celled species in the euphotic zone relative to small-celled species. Based on the physiology of microalgae, at least in conditions of balanced growth, it appears that small size is distinctly advantageous.

Consistent with the physiological advantages of small cells discussed above is the observation that small-celled picoplankton account for the dominant fraction of the algal biomass and productivity in most ocean regions (Joint & Pomroy 1983, Li et al. 1983, Takahashi & Bienfang 1983, Takahashi & Hori 1984). However, large phytoplankters do persist in the oligotrophic oceans (Sournia 1981) and there is no universal morphological (including size) attribute of the oceanic shade flora (Sournia 1982).

Apparently in contradiction to the observations of size dependence of μ_m in laboratory cultures of marine diatoms are the results of a recent study of growth rates of natural phytoplankton populations which did not reveal a size dependence of the maximum observed growth rate in 16 species of centric and pennate diatoms spanning a size range of 15 to 8700 μm^3 (Furnas 1982). Changes in environmental conditions over the course of the experimental period and differences in the number of observations of μ for the various species studied may explain the failure to observe a size dependence, although Furnas' (1982) observations

do raise the question of the importance of size in controlling microalgal growth rates in nature.

Exceptions to the general pattern of decreasing biomass in larger size classes include 'blooms' of large phytoplankters following stabilization of a nutrient-rich water column in the spring or associated with upwelling events. Some authors have suggested that large-celled phytoplankters may be better adapted to a variable environment because of reduced 'respiration' rates (Malone 1980b) or increased capacity to store nutrients (Turpin & Harrison 1980) which allow survival through adverse conditions.

The argument based on respiration rates may be spurious because it depends on an observed mass dependence of dark respiration rate which is often correlated with growth rate. The dark respiration rate will not necessarily be indicative of the maintenance energy requirement, but can be expected to have a value intermediate between r_m and $\mu \xi$.

As noted earlier in the discussion, small phytoplankters are characterized by higher maximum rates of nutrient uptake than large cells. In a pulsed nutrient regime small cells would be expected to have greater mass-specific nutrient uptake rates during the nutrient pulse, and so meet their nutrient demands at a faster rate than large cells. This could be offset by a greater capacity for nutrient storage in large cells that would allow these cells to continue to divide between nutrient pulses. There is, however, little evidence to support the assertion of greater fractional storage capacity in large cells (Raven 1984a). Similarities in elemental composition of large and small cells argue against changes in the ratio of stored nutrient to cell carbon.

An alternative explanation of the occasional dominance of large phytoplankters can be based on a consideration of the population dynamics of microalgae and zooplanktonic herbivores (Walsh 1976). Small microalgae are typically harvested by small invertebrates with mass-specific maximum growth rates which are the same magnitude as, or even greater than, microalgal growth rates (Banse 1982a). Increases in biomass of small microalgae should be rapidly followed by increases in the biomass of the small herbivores. In contrast, large microalgae are typically harvested by large herbivores with growth rates an order of magnitude lower than the growth rate of the microalgae. This divergence of growth rates of prey (algae) and predator (copepods) has been suggested to allow development of temporally separated blooms of both large-celled phytoplankton and copepods under conditions of large additions of nutrients to the euphotic zone. Small microalgae would not be able to take advantage of these nutrient inputs if net population increase is limited by grazing of a rapidly growing microzooplankton population. This hypothesis sug-

gests that large size provides a refuge from small predators in the microalgae, in contrast to the alternative hypothesis that small size offers a refuge from large predators in metazoan invertebrates (Brooks & Dodson 1965, Hall et al. 1976, Banse 1982b).

Walsh and coworkers (Walsh 1976, Walsh et al. 1978) have noted that blooms of large phytoplankton occur in the temporally more variable continental shelf regions where the storm cycle of about a week duration can account for a significant amount of the variance of water motion. The storm cycle produces a large input of nutrients on a time scale which allows uncoupling of the population dynamics of copepod herbivores and large-celled phytoplankton resulting in blooms. In the central oceanic regions this peak in the variance spectrum of water motion at the 1 wk period is missing and blooms of large-celled phytoplankton are less conspicuous. This hypothesis can only be confirmed after further investigation of the structure of planktonic food webs. Not inconsistent with this hypothesis is the observation of Landry & Hassett (1982) that 'small, naked ciliates graze little on the dominant phytoplankton types (e. g. diatoms) in coastal areas. Perhaps their greatest impact is on bacteria and microflagellates'.

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