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Scaling and transport kinetics in aquatic primary producers

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ABSTRACT: Geometry, size and shape are fundamentally important features of living organisms. It was hypothesised that in aquatic primary producers differences in geometry, shape and density would affect the relationship between dry mass, surface area and volume and that scaling relationships between rates of nutrient uptake and dry mass would vary depending on transport kinetics and nutrient concentration. Allometric relationships between dry mass (M) and volume (V), surface area (SA), growth rate and rates of nitrate uptake were determined using reduced major axis regressions. Volume scaled as $M^{1.03}$ and surface area as $M^{0.79}$ (and $V^{0.76}$) for aquatic primary producers. However, maximum growth rate, when expressed as g dry weight ind.$^{-1}$ d^{-1}, scaled as $M^{0.88}$. Maximum rates of nitrate uptake (expressed as µmol ind.$^{-1}$ h^{-1}) scaled similarly to growth ($M^{0.86}$). However, the scaling exponents ($M^{0.79}$) for rates of nitrate uptake at low concentrations and affinity (maximum uptake rate/the concentration of nutrient that gives half the maximum rate of uptake, V_{max}/K_m) were the same as the scaling exponent for surface area. Transport systems provide a useful approach to allometric relationships and illustrate that (1) scaling exponents for a given process can vary and (2) observed scaling exponents for transport are explicable through differences in the kinetics of transport systems. The maximum total surface area of the picoplankter *Prochlorococcus* and the kelp *Postelsia* per m^2 ocean surface are very similar, and the potential of marine 'leaf area indices' as a unifying concept is discussed.

KEY WORDS: Algae · Allometry · Macroalgae · Microalgae · Nitrate uptake

INTRODUCTION

Geometry, size and shape are cardinal features of all living organisms. Geometry refers to a type of solid, 3-dimensional object (e.g. sphere, cylinder, lamina), whereas shape specifies the relationship between dimensions within a particular geometric category. The aspect or axial ratio (e.g. ratio of length to diameter of a cylinder) is one measure of shape (Niklas 1994a, Dusenbery 1998). Though most geometric objects have different possible shapes, spheres are an exception. Moreover, for a geometry such as a cylinder, surface area $\propto$ mass$^{0.67}$ (assuming an isometric relationship between mass and volume) only when the aspect ratio is constant (i.e. the shape remains constant). Size, though some measure of quantity, can be and is defined in a variety of ways (e.g. mass, volume). However, there are a number of advantages and disadvantages associated with any given measure of size (Table 1).

The fact that a variety of environmental factors can affect the geometry, size and shape within a species, further emphasises the importance of these organismal properties. Changes in aspect ratio (or, more accurately, the length normalised width) occur in the diatom *Fragilariopsis kerguelensis* in response to iron limitation (Marchetti & Cassar 2009) and decreases in size (cell volume) and increases in their surface area:volume (SA:V) quotient occur in phytoplankton with decreased irradiance (Thompson et al. 1991), increased temperature (Montagnes & Franklin 2001), nutrient limitation (Harrison et al. 1977, Lynn

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Table 1. Advantages and disadvantages of various measures of size in aquatic primary producers

Parameter	Advantages	Disadvantages
Fresh mass	Would allow comparison with most of allometric literature	Extremely difficult to gain reliable values for phytoplankton. Variable (if known) relationship with dry mass in seaweeds
Dry mass	Easy to measure in seaweeds, but less so in marine microalgae unless care is taken to ensure that salt is removed	Ash (e.g. silica in diatoms, carbonate in calcifying organisms) can make up a substantial amount of dry mass. Composition of dry mass differs, with protein a major constituent in microalgae and carbohydrate in seaweeds
Volume	Relatively easy to measure in both microalgae and seaweeds, but values for latter are scarce	Vacuoles may occupy most of cell volume, but contribute little to biomass in some algae (e.g. diatoms, *Griffithsia*)
Carbon content	Universal constituent of living organisms	Depends on biochemical composition; carbon content varies from 40% in carbohydrate to 76% in lipid. Cell walls can have high or low carbon content. Carbon content as% dry mass can vary depending on ash content of organism

et al. 2000), zinc limitation (Varela et al. 2011) and the haploid phase (unicellular) of the life cycle of *Phaeocystis* (Ploug et al. 1999). Similar increases in SA:V (or decreases in thickness) occur in seaweeds with decreased irradiance (Norton et al. 1981, Wing et al. 2007), decreased water motion (Koehl et al. 2008) and nutrient limitation through the production of hyaline hairs (Raven 1981, DeBoer & Whoriskey 1983, Whitton 1988, Hurd et al. 1993, Steen 2003). Heteromorphic life histories also result in major changes in morphology in seaweeds (Lubchenco & Cubit 1980). Grazing or the threat of grazing alters morphology in microalgae (Beardall et al. 2009, Van Donk et al. 2011) and seaweeds (Lewis et al. 1987, Bracken & Stachowicz 2007, Diaz-Pulido et al. 2007).

The relationships between organism size and measures of organismal properties (metabolic rate, growth rate etc.) in general (Peters 1983) and, more specifically, in phytoplankton (Banse 1976) have a long history. Banse's (1976) original exponent of −0.25 for the relationship between phytoplankton volume and growth rate, was subsequently modified by the same author (Banse 1982) to −0.11. Since Banse's pioneering work, most exponents for the relationship between growth rate and cell volume are less than 0.25 (Laws 1975, Blasco et al. 1982, Sommer 1989, Mizuno 1991, Tang 1995, Finkel et al. 2010, Marañón et al. 2013 (for cells > 40 μm^3)), but there is one report of an exponent > −0.25 (Schlesinger et al. 1981).

Size explains a surprising amount of variability in biology, and many biological processes exhibit quarter-power scaling (West & Brown 2005). Scaling refers to the relationship between log body size (usually mass) and the log of a given biological variable. Basal metabolic rate (i.e. rate of maintenance respiration) over an impressive 10^{21}-fold range of organism size scales as a power law to mass with an exponent of 0.75 (West et al. 2002),

$$B = B_0 M^{0.75} \quad (1)$$

where B is the basal metabolic rate (watts), B_0 is a normalization coefficient (i.e. value of B where M = 1) and M is mass (usually fresh weight in g). One central feature of this relationship is that it does not conform to Euclidean geometry, which would give a scaling exponent of 0.67 (assuming that the organisms in question have the same shape and geometry). Given the power (in more than one sense) of these relationships (Brown et al. 2004) it would be useful to know how mass scaling relationships in a major and important group of photosynthetic organisms (aquatic primary producers) compare with other groups of organisms. The size range of algae and cyanobacteria (10^{17}) (Raven 1995), though less than that of all living organisms (10^{21}) is greater than that of other, frequently studied groups of organisms (e.g. ~10^5 for mammals) and encompasses a polyphyletic group of organisms. Moreover, their relative morphological simplicity, and the importance of their surface area relative to mass (most resources are acquired across the entire external surface of the alga or cyanobacterium rather than via specialised organs such as roots or alimentary canal) (Niklas 1994a, Raven 1995) make explanations of scaling relationships potentially simpler.

However, comparisons of the effects of size on the metabolism of phytoplankton and seaweeds are made difficult by the routine use of different units of measurement for both size and metabolic rate. With phytoplankton, size is generally measured as volume or carbon per cell, and metabolic rate is commonly expressed per cell. Neither carbon per cell nor metabolic rate is practicable for measurement of seaweeds (Table 1). Moreover, metabolic rate is usually expressed per unit dry weight. None of these measures of size allows for comparisons with other organisms where size is expressed as mass (fresh weight). However, the use of SA:V allows comparisons of metabolic rate in phytoplankton and seaweeds (Hein et al. 1995, Rees 2007) and is particularly useful where indeterminate growth is involved. Despite all this information, we know little about the scaling relationships between mass (rarely, if ever, used with aquatic primary producers), volume (used with phytoplankton) and SA:V (used with both phytoplankton and seaweeds). A further consideration is the extent to which both size and shape within aquatic primary producers influences scaling exponents. A common belief is that surface area scales to increasing mass with a scaling exponent of 0.67. This is certainly true if the geometry and shape are constant (e.g. sphere, cube) and there is an isometric relationship between mass and volume (Niklas 1994b). However, phytoplankton alone exhibit a range of geometries (Hillebrand et al. 1999) and shapes, and surface area scales as $V^{0.69}$ (Niklas 1994a).

Here I address 2 hypotheses. The first is that in aquatic primary producers differences in geometry, shape and density affect the relationship between dry mass, surface area and volume and prevent conformation to simple Euclidean geometry. The second is that scaling relationships between rates of nutrient uptake and dry mass vary depending on transport kinetics and nutrient concentration, with the exponent for maximum uptake rate achieved at saturating concentrations of the nutrient (V_{max}) being close to that for growth rate.

MATERIALS AND METHODS

Data

I searched the literature for mass (dry weight), volume, surface area, maximum growth rates, and kinetic parameters (the concentration of nutrient that gives half the maximum rate of uptake, K_m, and V_{max}) for nitrate uptake for marine and freshwater primary producers (i.e. marine and freshwater phytoplankton and seaweeds) (see Supplement at www.int-res.com/articles/suppl/m509p103_supp.xls). Where only linear dimensions were provided for phytoplankton, appropriate formulae (Hillebrand et al. 1999) were used to calculate surface area and volume. Growth rate data also included values for freshwater macrophytes. Wherever possible, values for mass and other variables were obtained from the same source; this was more common for volume and growth rate data. However, most data for dry mass were obtained from sources other than the metabolic data. When there was more than one published value for dry mass, mean values were used. It should be noted that I only used data for species for which values for dry mass and some other measure (e.g. volume, growth rate) were available. This limited the total number of data points. Rates were usually expressed per cell for phytoplankton and per g dry weight for seaweeds. Consequently, rates for individual seaweeds were calculated as the rate per g dry weight × individual dry weight. If there were a number of unidentified species from a given genus (e.g. *Chlorella*), they were treated as different species, as were strains of *Prochlorococcus* and *Synechococcus*. All metabolic rates (i.e. uptake and growth) were converted to rates at 20°C, assuming a Q_{10} of 1.88 (Eppley 1972).

Growth rate and daily production

Maximum specific growth rates (μ_{max}) are expressed as d^{-1}. Data provided as doublings per day (base 2) were converted to μ by multiplying by ln 2 (= 0.6931). Where there was more than one reported value for growth rate, the highest values were used. Daily production is the product of growth rate and mass (g dry weight $ind.^{-1}$ d^{-1}).

Nitrate uptake

The 2 kinetic parameters derived from the hyperbolic relationship between nutrient concentration and rates of nutrient uptake are K_m and V_{max}. Rates of nitrate uptake at 1 nM were calculated from the Michaelis-Menten formula:

$$\frac{(V_{max})\ (\text{nitrate concentration})}{K_m + \text{nitrate concentration}} \quad (2)$$

Data were used only if both K_m and V_{max} values were provided.

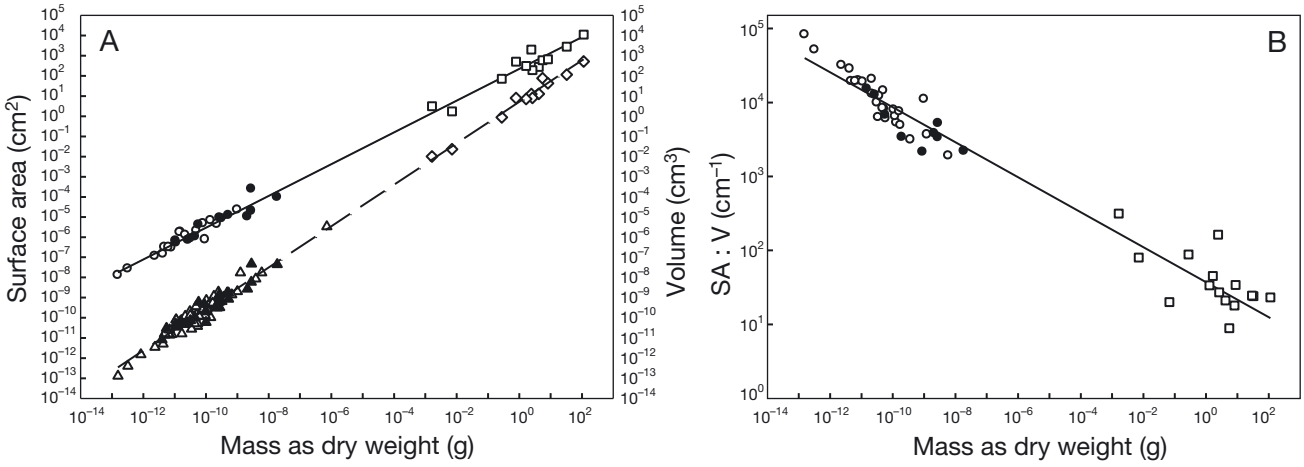

Fig. 1. (A) Surface area (cm^2) for marine phytoplankton (○), freshwater phytoplankton (●) and seaweeds (□) and volume (cm^3) for marine phytoplankton (△), freshwater phytoplankton (▲) and seaweeds (◇) versus mass as dry weight (g). Reduced major axis regression equation and coefficient of determination for surface area (solid line) are $y = 2.35x^{0.79}$, $r^2 = 0.994$, p (slope = 0) < 0.001 and for volume (dashed line) they are $y = 0.72x^{1.03}$, $r^2 = 0.994$, p (slope = 0) < 0.001. (B) Surface area:volume (cm^{-1}) for marine phytoplankton (○), freshwater phytoplankton (●) and seaweeds (□) versus mass as dry weight (g). Reduced major axis regression equation and coefficient of determination are $y = 1.62x^{-0.24}$, $r^2 = 0.968$, p (slope = 0) < 0.001

Statistical analysis

Reduced major axis (RMA) regression (Sokal & Rohlf 1995) was used to describe relationships between log dry mass and log morphological or metabolic parameters. For these analyses the line-fitting package SMATR Ver. 2.0 (Warton et al. 2006; https://github.com/dfalster/smatr/) was used. Analysis of covariance was used to test for homogeneity of slopes and intercepts when different groups of organisms were pooled for regression analysis.

RESULTS

There was a strong positive relationship between log mass (M, g dry weight) and log volume (V, cm^3) (Fig. 1A, Table 2). The scaling exponent was 1.03 (Table 2), suggesting that there was a decrease in density (from 0.45 to 0.17 g dry mass cm^{-3} across the range of M) with increasing M and the 95% confidence limits did not include 1.0 (Table 2). In contrast, SA (cm^2) scaled as $M^{0.79}$ (Fig. 1A, Table 2) and $V^{0.76}$. The relationship between log M and log SA:V (cm^{-1}) had a scaling exponent of –0.24 (Fig. 1B, Table 2).

Maximum growth rate (d^{-1}) scaled as $M^{-0.13}$ (Fig. 2A, Table 2), and when expressed as g dry weight $ind.^{-1}$ d^{-1} as $M^{0.88}$ (Fig. 2B, Table 2). However, it is noticeable that the picoplankton (cells <10 pg dry mass) had low growth rates relative to their mass (Fig. 2, dashed line indicates 10 pg). If the picoplankton are removed, the slopes and intercepts are homogenous, but the change in the RMA scaling relationship was minor ($y = 1.287x^{-0.139}$ without picoplankton com-

Table 2. Scaling parameters and statistics determined by reduced major axis (RMA) regression for relationships between aquatic primary producer volume (cm^3), mass (g dry weight), cell or tissue surface area (cm^2), or surface area:volume (cm^{-1}), and growth rate (d^{-1}), daily production (g dry weight $ind.^{-1}$ d^{-1}), maximum rate of nitrate uptake (V_{max}) (µmol $ind.^{-1}$ h^{-1}), rate of nitrate uptake at an external concentration of 1 nM (V_1) (µmol $ind.^{-1}$ h^{-1}) and maximum rate of nitrate uptake/concentration of nutrient giving half the maximum rate of uptake (V_{max}/K_m) for nitrate uptake versus mass

Parameters	N	r^2	Slope	95% CI	Intercept	95% CI
Volume ∝ mass	90	0.994	1.029	1.013 to 1.046	0.719	0.564 to 0.873
Surface area ∝ mass	41	0.994	0.788	0.768 to 0.807	2.345	2.175 to 2.515
Surface area: volume ∝ mass	41	0.968	–0.241	–0.256 to –0.228	1.615	1.493 to 1.738
Growth rate ∝ mass	96	0.814	–0.133	–0.145 to –0.121	–1.285	–1.390 to –1.179
Daily production ∝ mass	96	0.996	0.883	0.871 to 0.895	–1.166	–1.271 to –1.061
Nitrate uptake (V_{max}) ∝ mass	18	0.995	0.860	0.829 to 0.892	1.157	0.898 to 1.416
Nitrate uptake (V_1) ∝ mass	18	0.983	0.794	0.740 to 0.851	–2.824	–3.286 to –2.362
Nitrate uptake (V_{max}/K_m) ∝ mass	18	0.983	0.794	0.740 to 0.851	0.176	–0.286 to 0.638

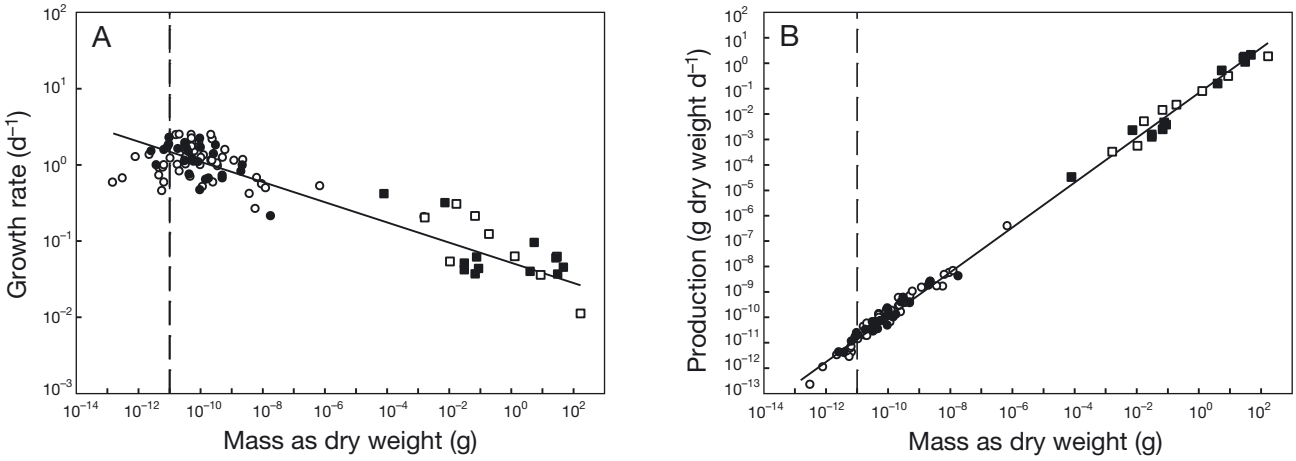

Fig. 2. (A) Growth rate (d^{-1}) and (B) production (g dry weight ind.$^{-1}$ d^{-1}) for marine phytoplankton (○), freshwater phytoplankton (●), seaweeds (□) and freshwater macrophytes (■) versus mass (g dry weight). Dashed line indicates where values less than this (10 pg dry mass) correspond to picoplankton as defined in the 'Results'. Reduced major axis regression equations and coefficients of determination are (A) $y = -1.29x^{-0.13}$, $r^2 = 0.814$, p (slope = 0) < 0.001 and (B) $y = -1.17x^{0.88}$, $r^2 = 0.996$, p (slope = 0) < 0.001

pared with $y = 1.285x^{-0.133}$ with picoplankton). If growth is balanced, one would expect all metabolic activities to scale with similar exponents. Other metabolic activities (all expressed as µmol ind.$^{-1}$ h^{-1}) scaled similarly to growth (when expressed as g dry weight ind.$^{-1}$ d^{-1}); maximum rate of photosynthesis scaled as $M^{0.88}$ (data not shown), and maximum rate of nitrate uptake as $M^{0.86}$ (Fig. 3, Table 2). Affinity (V_{max}:K_m) scaled as $M^{0.79}$ for nitrate uptake (Fig. 3, Table 2). There was also an identical decrease in the scaling exponent for rates of nitrate uptake at an external concentration of 1 nM ($M^{0.79}$) (Table 2) and the exponent was significantly different (ANCOVA $F_{1,33} = 5.61$, p = 0.024) from that for maximum rate of nitrate uptake.

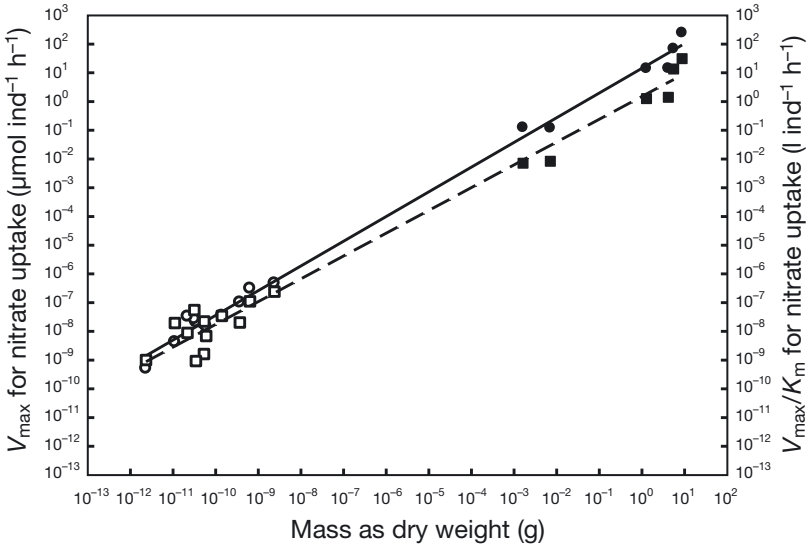

Fig. 3. Rate of nitrate uptake (µmol ind.$^{-1}$ h^{-1}) for phytoplankton (□) and seaweeds (●) at V_{max} (○) or V_{max}/K_m (l ind.$^{-1}$ h^{-1}) (■) versus mass (g dry weight). Reduced major axis regression equation and coefficient of determination are $y = 1.16x^{0.86}$, $r^2 = 0.995$, p (slope = 0) < 0.001 for V_{max} and $y = 0.18x^{0.79}$, $r^2 = 0.983$, p (slope = 0) < 0.001 for V_{max}/K_m. V_{max}: maximum rate of nitrate uptake; K_m: concentration of nutrient giving half the maximum rate of uptake

DISCUSSION

The maximum rates of nitrate uptake scale as $M^{0.86}$. In contrast, at very low external concentrations of these nutrients, rates scale as $M^{0.79}$, which would occur if the rate of uptake was directly proportional to surface area. Transport systems provide a useful approach to allometric relationships and illustrate that (1) scaling exponents for a given process can vary (Finkel et al. 2004, Glazier 2005), and (2) observed scaling exponents for transport are explicable through differences in the kinetics of the transport systems when expressed per unit surface area (Rees 2007).

Effect of geometry, shape and density on relationships between dry mass, volume and surface area

Based on Euclidean geometry and constant density, surface area should scale as $M^{0.67}$. However, this

assumes that the organisms in question have the same geometry and shape as well as density. Aquatic primary producers exhibit a range of geometries and shapes, and surface area scaled as $M^{0.79}$ and $V^{0.76}$. It has been shown elsewhere (Niklas 1994a) that there is a decrease in density with increasing mass (as carbon) in phytoplankton, suggesting that V must scale to M with an exponent greater than 1.0. Therefore, although SA:V decreases with increasing size, the relative (to V) decrease in surface area is partially offset by the given volume containing less dry mass per unit volume. Consequently, with increasing mass among algae and cyanobacteria, changes in morphology (geometry and shape) and density result in a greater increase in surface area (relative to mass) than would have occurred had they maintained a constant morphology and density with increase in size.

Volume scales as $M^{1.03}$, suggesting that density (g dry mass cm^{-3}) decreases with increasing size. One implication of this relationship is that SA:V decreases more than SA:M does with increasing size. This raises the issue of whether volume or dry mass is more important as a determinant of metabolic processes. With decreased density, the most important consideration is likely to be transportation distance, and this will become more pronounced as volume increases. For example, assuming that the relative proportion of biomass constituents remains constant, there would be greater distances between ribosomes in less dense cells and tissues, which would potentially increase the transit times for constituents such as mRNA involved in protein synthesis (Beardall et al. 2009). In contrast, with decreased density there would be less dry mass to double per unit volume, which may counteract some of the decrease in metabolic rate associated with an increase in size. However, there is a 2.6-fold range in density, which compares with a 220-fold range in growth rate, suggesting that any contribution made by decreased density is relatively minor.

Size and growth rate

Maximum growth rate (d^{-1}) scaled as $M^{-0.13}$ and when expressed as g dry weight $ind.^{-1}$ d^{-1} as $M^{0.88}$. However, it is noticeable that with picoplankton, defined as cells < 10 pg dry mass, growth rate increased with dry mass. This increase in maximum growth rate with increasing size within the picoplankton is well documented (Raven 1986, 1994, Bec et al. 2008, Marañón et al. 2013) and explained (Raven 1986, 1994, 1998); as photosynthetic cells become smaller, non-scalable components (genome and membranes) assume a greater proportion of the total volume leaving less room for essential and scalable components (enzymes, light-harvesting pigment-protein complexes), leading to lower maximum growth rates.

The relationship between volume and phytoplankton (not just a specific group such as diatoms) growth rate yields exponents that range from −0.06 (Finkel et al. 2010), −0.08 (Sommer 1989), −0.14 (Tang 1995), to −0.32 (Schlesinger et al. 1981). The relationship reported in the present study (including macroalgae) is comparable to the lower exponents and scaled as $M^{-0.13}$ or $V^{-0.10}$, suggesting that quarter-power scaling does not apply, partly because of the diversity of geometries and shapes involved.

Size, boundary layer and nitrate transport

Since the classic paper by Munk & Riley (1952), which highlighted the role of physical processes in the uptake of nutrients by phytoplankton, there have been a number of additions and modifications to their approach. Following the addition of the biological component of transporter kinetics (Pasciak & Gavis 1974, Gavis 1976), other refinements have been made (Aksnes & Egge 1991, Ploug et al. 1999, Sanford & Crawford 2000, Armstrong 2008).

All of these models, despite different approaches, share 2 basic conclusions (Bonachela et al. 2011). The maximum rate of uptake expressed per individual is not physically constrained, but as the concentration decreases towards ecologically realistic concentrations the boundary layer becomes increasingly important as a constraint on uptake. With the latter there are 2 important considerations. The first is that the smaller the organism, the less the effect of the boundary layer, a layer of relatively motionless water surrounding a solid body across which a nutrient must diffuse (Niklas 1994b, Raven 1995, 1998, 1999), and, secondly, the effect of an increased boundary layer is to increase the apparent K_m (Ploug et al. 1999), and, consequently, decrease affinity.

Maximum rates (V_{max}) of nitrate uptake scale as $M^{0.86}$, because the V_{max} per cm^2 surface area is greater in large algae (seaweeds) than in unicellular algae and cyanobacteria (Rees 2007), and is close to the relationship for growth rate ($M^{0.88}$). We do not know what constrains maximum growth rate, but it clearly is not the available surface area of the organ-

ism. V_{max} is the rate at infinite external concentration where any effect of the boundary layer is likely to be minimal (Sanford & Crawford 2000, Smit 2002). The scaling exponent for uptake at a low substrate concentration (1 nM) decreases from $M^{0.86}$ to $M^{0.79}$ for nitrate uptake, and the decrease in slope is attributable to a greater decrease in the rate of uptake in seaweeds as concentration decreases. The reason for this is that as algal size increases, the boundary layer becomes an increasing constraint on the rate of uptake at low concentrations. The net effect is to increase the apparent K_m for nitrate uptake (Edwards et al. 2012, Marañón et al. 2013) and decrease affinity. These changes result in the increase in rate of uptake at low concentrations matching the increase in surface area with increasing size of alga; in other words, the greater V_{max} per unit surface area in seaweeds is cancelled out by the increase in the boundary layer in these larger algae at low external concentrations of nitrate, and the rate of nitrate uptake per unit surface area at low external concentrations is largely invariant across the 10^{17}-fold size range of algae.

Nevertheless, there are 2 further considerations. The first is that the data for unicellular algae are for cultured species growing under largely defined conditions, whereas the data for seaweeds are for species collected from the field and, consequently, of largely undefined physiological status. The second is that, although what is being measured is clearly uptake across the cell membrane, the rate is associated with assimilation (the internally controlled uptake phase or V_i) (Harrison et al. 1989, Barr et al. 2004). Moreover, nutrient uptake by *Macrocystis integrifolia* in wave-exposed and wave-sheltered sites is rarely mass transport limited (Stevens et al. 2003), and both growth rate and ammonium uptake saturate at low flow rates in *Ulva pertusa* (Barr et al. 2008).

The relationship between volume and rates of nitrate uptake has been investigated in phytoplankton (Litchman et al. 2007, Edwards et al. 2012, Marañón et al. 2013), but not seaweeds. However, none of these studies explicitly relate uptake data to surface area. Litchman et al. (2007) report that the maximum rate of nitrate uptake by phytoplankton scales as $V^{0.67}$ (this includes a discussion based on the incorrect assumption that phytoplankton have identical geometries); based on an increased amount of data Edwards et al. 2012 report that it scales as $V^{0.82}$ (equivalent to $M^{0.84}$), whereby the confidence intervals do not exclude the exponent (0.86) reported in the present study. Edwards et al. (2012) also report that affinity has an exponent of $V^{0.75}$, almost identical to the exponent for surface area ($V^{0.76}$) reported in the present study. However, there is no way of explicitly relating their data to surface area. The same is true for Marañón et al. (2013) where V_{max} scales to $V^{0.97}$ (according to my RMA analysis and ignoring their data for *Prochlorococcus*, which is for ammonium uptake), but the confidence limits (0.89–1.11 converted to M, assuming V scales as $M^{1.03}$) marginally overlap with the confidence limits reported in the present study. Again, it is not possible to relate these data to surface area.

A greater maximum rate of uptake per cm^2 surface area in seaweeds (compared with phytoplankton) could be achieved by (1) increasing the number of transporters with similar kinetic properties per unit surface area, (2) altering the kinetics (e.g. increased V_{max}) of a constant number of transporters per unit surface area, (3) altering the proportions of 2 or more transporters with different kinetics and/or (4) increasing net transport by decreasing the rate of efflux of the nutrient. Although increasing the number of transporters is possible, there would be an upper limit to the number of transporters per unit area of cell membrane unless other transporters were lost. For yeast cells, there is evidence that space in the cell membrane is limited for constitutive transporters, but less so for inducible transporters (Hennaut et al. 1970). The overwhelming majority of measurements of nutrient transport in algae measure net uptake. Evidence from higher plants suggests that there are separate transport proteins that catalyse influx and efflux of a nutrient. For example, there is considerable physiological evidence for influx and efflux of nitrate (Crawford & Glass 1998). The genes for a number of high and low affinity nitrate influx transporters have been isolated (Tsay et al. 2007) and a nitrate efflux transport protein has also recently been isolated (Segonzac et al. 2007). There is no evidence for the existence of any efflux transporters in algae, though it would be surprising if they did not exist. Given their greater SA:V, passive efflux is more likely to be a problem for microalgae than seaweeds, but, given our ignorance of the characteristics of algal efflux transporters, it does not follow that this equates to a greater efflux per cm^2 surface area in phytoplankton. Any or all of the mechanisms by which seaweeds could increase the rate of uptake per unit area of cell membrane listed above are currently possibilities and none have been excluded.

Ecological implications

Based on the analysis of Sanford & Crawford (2000), mass transfer control is less likely in high-energy, high-nutrient environments and for algae with low V_{max}:K_m. Consequently, the extent of mass transfer control will depend on the environment of the seaweed, with algae in high-energy (Leigh et al. 1987) and/or nutrient-rich environments (e.g. upwelling regions) less likely to be affected. One mechanism for minimising the impact of the boundary layer (and which is under the control of the organism) is to decrease V_{max}:K_m (Sanford & Crawford 2000). V_{max}:K_m (with V_{max} expressed as µmol ind.$^{-1}$ h^{-1}) scales as M$^{0.79}$ for nitrate uptake, which is very close to the scaling for surface area. This suggests that the amount of surface area presented is a critical determinant of the ability of an alga, particularly seaweeds, to acquire nutrients and grow under most, resource-limited conditions in nature. However, the relationship between dry mass and V_{max}:K_m depends on the units for V_{max} (units for K_m are consistently expressed as µM). For example, if V_{max} is expressed as µmol ind.$^{-1}$ h^{-1}, V_{max}:K_m increases markedly with dry mass, but decreases with dry mass when V_{max} is expressed as µmol g^{-1} dry mass h^{-1}. Ideally, one would like information on the kinetic characteristics of the relevant transport protein, but in its absence the best approach would be to express V_{max} per unit surface area, as this is where the transporter is located and acts and where the boundary layer impedes access to nutrients. The diffusion boundary layer thickness in spherical cells below about 50 µm radius is equal to the radius of the cell (Raven 1998). In macroalgae the diffusion boundary layer thickness is greater and ranges from 100 to 10200 µm (Raven & Hurd 2012). Moreover, even if seaweeds had evolved transport systems with decreased V_{max}:K_m, this mechanism would not solve the problem of acquiring nutrients, as minimising the impact of the boundary layer would lead to a decreased intrinsic ability to acquire nutrients when they are present at low concentrations.

Marine 'leaf area index'

Leaf area index (LAI, total upper area of leaves per unit ground area) is a measure of terrestrial canopy foliage used in a range of terrestrial physiological and biogeochemical studies (Asner et al. 2003). The picoplankter *Prochlorococcus* and the kelp *Postelsia palmaeformis* represent opposite extremes of the size range in aquatic primary producers. From an ecological point of view it is interesting that they have similar 'leaf' or surface area indices (i.e. integrated total (both sides) area per m^2 ocean surface or 2 × LAI), although the dry mass of *Postelsia* per m^2 ocean surface is about 10^3 times greater than that of *Prochlorococcus*. *Prochlorococcus* reaches densities of 6.7 × 10^{13} cells m^{-2} ocean surface (Liu et al. 1997). A dry mass of 0.155 pg per cell (Shaw et al. 2003) and cell surface area of 0.92 µm^2 (Blanchot et al. 2001) equates to 10 g dry mass *Prochlorococcus* m^{-2} ocean surface and 62 m^2 *Prochlorococcus* surface area m^{-2} ocean surface. In comparison, maxima for *Postelsia* are 7300 g dry mass m^{-2} ocean surface and 68 m^2 surface area m^{-2} ocean surface (Leigh et al. 1987). Cell or tissue areal rates of ammonium assimilation required to sustain growth rates measured in natural populations are remarkably similar for both phytoplankton and macroalgae (Rees 2007), which suggests that rates of ammonium assimilation per m^2 ocean surface may also be similar, irrespective of the size of the dominant primary producer. This suggests that a m^2 of ocean may be functionally similar for picoplankton- and seaweed-dominated waters and serves to reinforce the potentially unifying importance of cell surface area in the ecology of aquatic photosynthetic organisms.

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