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Size-dependent growth rates in eukaryotic and prokaryotic algae exemplified by green algae and cyanobacteria: comparisons between unicells and colonial growth forms

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The size dependency of maximum growth rates was investigated in cyanobacteria and in green algae (Chlorophyta). Both unicellular and colony-forming species were included in the study. Significant allometric relationships were found between size and maximum growth rate for both cyanobacteria and green algae. The size-dependent growth could be described by the same scaling exponent in both cyanobacteria and green algae, but in both cyanobacteria and green algae only unicells evinced size-dependent growth rates—there was no relationship between colony size and growth rate in colonial forms of cyanobacteria and green algae. It is concluded that the colonial growth form represents an evolutionary adaptation to escape the negative effects of size-dependent growth, while retaining the positive effects of increased size, e.g. a decreased grazing pressure.

INTRODUCTION

Strong scaling relationships have often been shown between metabolic rates or growth on one side and size on the other. They can be described by an allometric power function:

$$\text{Rate} = aW^b$$

where Rate can be any metabolic rate or the growth rate and W is the size or body mass of the organism. If the rate is a specific metabolic rate or the specific growth rate, then the exponent b is usually found to be –0.33 or –0.25 (Peters, 1983; Geider *et al.*, 1986). The phenomenon has probably been most thoroughly studied in animals (Peters, 1983), but has been documented for photosynthetic organisms from unicellular algae to trees as well (Niklas, 1994; Nielsen *et al.*, 1996).

It has been found that different types of animals (unicells, poikilotherms and homeotherms) display scaling relationships with the same slope and thus with basically the same dependence of size on metabolism, but with some offset of the line, corresponding to varying metabolic costs for different types of animals with the same size (lowest for unicells, highest for homeotherms) (Hemmingsen, 1960). Research on allometric scaling in photosynthetic organisms has focused on documenting scaling relationships, covering a broad range of photosynthetic organisms from unicellular algae to trees and cacti with very thick photosynthetic tissue (Enríquez *et al.*, 1996; Nielsen *et al.*, 1996). Any systematic differences between unicellular algae, colony-forming algae and multicellular algae and plants have not so far received sufficient attention.

Earlier studies of allometric scaling relationships on specific taxonomic groups of algae led to the conclusion that different taxonomic groups displayed different scaling relationships and that some groups displayed very

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weak relationships or none at all (Banse, 1976, 1982b; Blasco *et al.*, 1982; Geider *et al.*, 1986; Chisholm, 1992). Similarly, different scaling relationships have been shown for prokaryotic photosynthetic organisms (cyanobacteria) and eukaryotic photosynthetic organisms (Shuter, 1978; Niklas, 1994). This have led to the statement that scaling exponents in photosynthetic organisms evince phyletic dependence (Niklas, 1994).

The exact nature of the scaling relationships has also been debated. A scaling exponent of –0.33 is predicted if size-dependent growth and metabolism are controlled by the relationship between surface, through which exchange of energy and matter with the surroundings take place, and volume in which all metabolic processes take place (Brown *et al.*, 2000). This has long been known and is often referred to as the surface-law (Sarrus and Rameaux, 1839; Rubner, 1883). It has been argued that the scaling exponents that are actually found are closer to –0.25, referred to as Kleibers rule (Kleiber, 1932; Brown *et al.*, 2000) and a mechanistic model for the –0.25 scaling exponent based on first principles has been proposed (West *et al.*, 1997). It has, however, recently been shown that the scaling of the basal metabolic rate in animals follows the surface law rather than Kleibers rule (White and Seymour, 2003). Organisms change form while increasing in size. Small organisms are nearly spherical, but if large organisms also were spherical, they would have very long diffusion pathways from the surface of the organisms. It has therefore been argued that morphological isometry is not beneficial for the passive diffusion of substances (Niklas, 1994). Probably due to an evolutionary response to these constraints organisms become flatter with increasing size (Niklas, 1994) or have developed other anatomical and morphological adaptations (West and Brown, 2005). The first response is seen in photosynthetic organisms in flat thalli and flat leaves in macroalgae and higher plants, and the second response is seen in mass flow transport systems (lungs, blood etc.) in animals.

In this study changes in allometric scaling relationships with increasing organism size and complexity will be considered, and the question of phyletic dependence and the nature of the scaling exponent addressed, based on data on green algae (Chlorophyta) and cyanobacteria. Although it has previously been shown that the same scaling exponent can be used to describe size-dependent growth over a range of photosynthetic organisms from microalgae to trees (Nielsen and Sand-Jensen, 1990; Nielsen *et al.*, 1996), it has been argued, as mentioned above, that the scaling exponent of different algae groups vary depending on their phyletic affiliation (Niklas, 1994). Green algae and cyanobacteria were chosen for this study because especially the green algae, but also the cyanobacteria, show a large variety in size over 3 orders of magnitude (from <1 μm to ~1 mm) and a variety in complexity with both unicellular and colony-forming species. Using these two groups of organisms allows effects of size and complexity to be tested without confounding effects of phyletic affiliation.

METHOD

The majority of data for this analysis were drawn from the literature. A total of 407 data points covering the species listed in Appendix 1 were drawn from the sources listed in Appendix 2. A minor portion of these data points (164 data points) were used in previous work on broad-range allometric scaling in photosynthetic organisms (Enríquez *et al.*, 1996; Nielsen *et al.*, 1996), but as those papers had a different focus, the data has not previously been used to elucidate the questions put forward here. The literature data have not been recalculated, but in some cases, where exact numbers were not given in text or tables, they have been acquired by digitizing figures in the papers. In a number of cases where only growth rates were given, they have been supplemented and paired with data on cell or colony size, drawn from the taxonomic literature (Tikkanen and Wilén, 1992).

To supplement the literature data, a total of 19 species of green algae (Chlorophyta) and nine species of cyanobacteria were grown in the laboratory as part of this work. These species comprised unicells as well as colony-forming species. All species were drawn from the Culture Collection of Algae at the University of Texas at Austin (UTEX) (Starr and Zeikus, 1993). The cultures were grown under conditions aimed at achieving optimal growth so that the measured growth rates would depend on intrinsic properties of the species and on internal cell processes rather than on external limiting factors. The cultures were grown axenically at 17°C in continuous light at a photon flux density of 200 μmol m^{-2} s^{-1}. The light sources used were fluorescent tubes (Philips TLD Aquarelle and Philips TLD 90 Warm White). The algae were grown in round-bottomed flasks and were kept in suspension by bubbling with atmospheric air that had been passed through 0.3 μm glass microfiber filters (Whatman Hepa-Vent) to keep the cultures axenic. The growth media used were those used for each species at UTEX (Starr and Zeikus, 1993) so that several different media were used in the experiment. Please see Starr and Zeikus (Starr and Zeikus, 1993) for details or refer to the UTEX homepage (http://www.bio.utexas.edu/research/utex/). To ensure that nutrients were not exhausted and to keep the cultures in the exponential

growth phase at low cell densities the media were frequently replenished. The intervals depended on the growth rate of the culture in question.

Growth rates were obtained by repeated counting of cells and colonies under the microscope using appropriate magnification and counting chambers. Only cultures found to be in the exponential growth phase were included in the data. Cell or colony density was counted with 1–5 days intervals, depending on the growth rate of the particular species. Several culture batches were run for each species and the data used in this context as maximal growth rates are the highest growth rates found. The size of cells and colonies were obtained by measuring under the microscope using an eyepiece with a calibrated micrometer. Sizes were measured during the counting of cells and colonies, and at least 100 cells or colonies were measured at each instance. Values given for sizes are the average values found during the growth experiment that yielded the maximum growth rate for that species. The appropriate measurement of size for the purpose of this study was assumed to be the thickness or minor axis of cells or colonies as this has previously been shown to be a good determinant of maximum growth rate (Nielsen *et al.*, 1996).

The relationships between cell or colony size and maximum growth rate were described using least-squares regression analysis on log-transformed (base 10) variables. Logarithmic transformation of both variables was performed in order to transform the allometric power function $Y = aX^b$ to a straight line ($\log Y = \log a + b \log X$). Differences in the scaling of growth rate to size among various subsets of data were examined using analysis of covariance (ANCOVA) (Sokal and Rohlf, 1995), and differences between the calculated regression coefficients (values of b) and theoretical values were tested using Student's t-test (Sokal and Rohlf, 1995).

RESULTS

Statistically significant relationships between cell or colony size and maximum growth rate are found for both green algae (Chlorophyta) and cyanobacteria (Fig. 1). The existence of very small colonial forms is a consequence of size being measured as thickness because the filaments of many filamentous algae are only one cell thick. The slopes and elevations of the lines found for green algae ($b = -0.219$, $a = -0.103$, Fig. 1, Table I) and for cyanobacteria ($b = -0.202$, $a = -0.127$, Fig. 1, Table I) are not significantly different when tested by analysis of covariance ($P > 0.05$), so eukaryotic green algae and prokaryotic cyanobacteria apparently follow the same allometric relationship between size and maximum growth rate. The slopes of –0.219 and –0.202, respectively, are not in accordance with the so-called surface-law as these values are significantly different from the value of –0.33 predicted by the surface-law (t-test, $P < 0.001$). They are, however, not significantly different from a value of –0.25 predicted from Kleibers rule ($P > 0.05$). When the datasets are broken down into subsets containing unicellular forms and colony-forming forms respectively (Fig. 1, Table I), it becomes clear that the relationship between size and growth rate is defined by strong relationships between cell size and growth rate in the unicellular forms. Both unicellular green algae and unicellular cyanobacteria show significant relationships between cell size and maximum growth rate with steeper slopes (–0.364 and –0.258, respectively, Fig. 1, Table I) than was found when colonial forms were included in the comparisons. Again, there is no significant difference between the two groups with regard to slope and elevation of the regression lines as analysed with analysis of covariance ($P > 0.05$), but in contrast to the situation with the total data sets, the unicells are in accordance with both the surface-law and Kleibers rule, as the slopes are not significantly different from either –0.25 or –0.33. The relationship between cell size and maximum growth rate is somewhat weaker for unicellular cyanobacteria than for unicellular green algae ($r^2 = 0.067$ and 0.144, respectively), due to the wide range of growth rates reported as maximum growth rates for picoplanktonic cyanobacteria (Fig. 1). When only colony-forming forms are considered, no relationships between colony size and maximum growth rate for either green algae or cyanobacteria are found (Fig. 1, Table I). The slopes of –0.082 and –0.035 for green algae and cyanobacteria respectively (Table I) are not significantly different from zero ($P = 0.289$ and $P = 0.537$).

DISCUSSION

The data for green algae and cyanobacteria that are analysed in this study clearly show that eukaryotic green algae and prokaryotic cyanobacteria follow the same allometric relationship. This is in good agreement with previous work by this author and co-workers, who found that one scaling exponent can describe size-dependent growth over the whole range of photosynthetic organisms from unicellular algae over macroalgae and submerged angiosperms to terrestrial plants including trees and cacti (Nielsen and Sand-Jensen, 1990; Nielsen *et al.*, 1996), but disagrees with some of the earlier reviews of size-dependent growth in phytoplankton, dealing

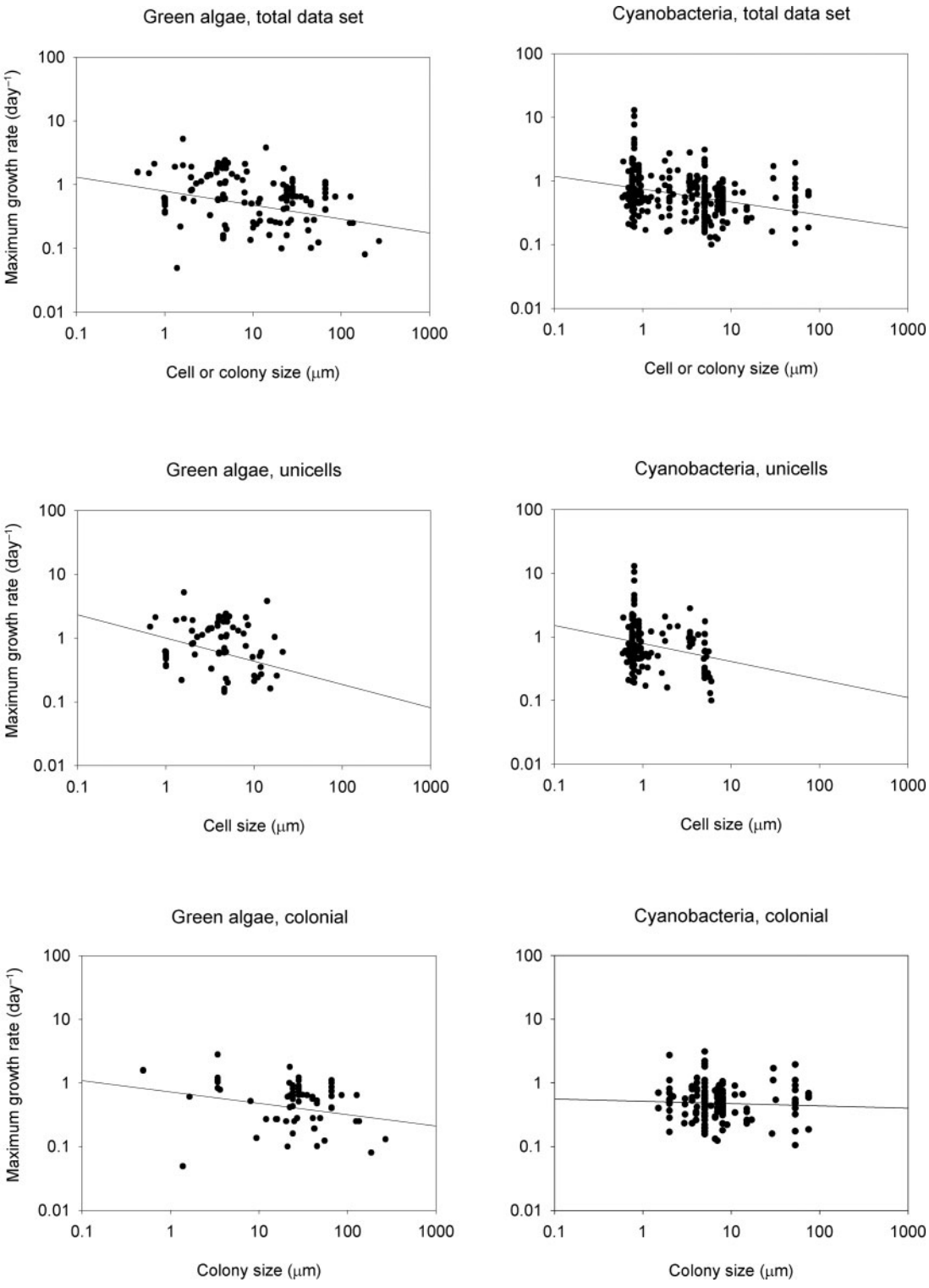

Fig. 1. Relationships between maximum growth rates and cell or colony size measured as thickness/length of the minor axis for green algae and cyanobacteria. The relationships for the total data sets for each taxonomic group are shown as well as for data subsets of unicells and colonies for each group. The lines are the fitted least-squares regressions lines (Table I).

Table I: Slope, constant and regression statistics for the least-squares regressions lines in Fig. 1

Algal group	Slope	Constant	*n*	r^2	*P*
Green algae, total data set	–0.219 ± 0.086	–0.103 ± 0.100	211	0.107	<<0.0001
Cyanobacteria, total data set	–0.202 ± 0.061	–0.127 ± 0.041	336	0.114	<<0.0001
Unicellular green algae	–0.364 ± 0.165	0.004 ± 0.133	114	0.144	<<0.0001
Unicellular cyanobacteria	–0.258 ± 0.137	–0.105 ± 0.045	189	0.067	<<0.0001
Colonial green algae	–0.082 ± 0.151	–0.273 ± 0.227	97	0.013	0.289
Colonial cyanobacteria	–0.035 ± 0.112	–0.293 ± 0.106	147	0.003	0.537

All regressions are on double logarithmically transformed data, so the line is: $\log_{10} Y = a + b \log_{10} X$. The slope and the constant are given ± standard error.

mainly with diatoms and dinoflagellates, that find different scaling exponents in different taxonomic groups (Banse, 1976, 1982a; Geider *et al.*, 1986). Differences in the scaling of size-dependent growth rates among various taxonomic groups of algae can have profound ecological consequences and merit further studies. Although there is no evidence for phyletic dependence (Niklas, 1994) when comparing green algae and cyanobacteria in this study, it is clear from Fig. 1 that picophytoplankton can achieve highly variable maximum growth rates within a very limited size range. It has previously been suggested that picophytoplankton may deviate from the general allometric relationships (Raven, 1994), because a large fraction of their biomass is occupied by non-scalable components such as the genome, the plasmalemma and other membranes. Therefore a smaller fraction of the biomass is allocatable to core metabolic processes, determining the scaling exponents (Raven, 1998, 1999). In this study, no size-dependent growth is found within this group alone, but when compared with other cyanobacteria they, as a group, abide by the same allometric laws.

When comparing unicells alone, it becomes clear that unicells show a stronger relationship for size-dependent growth than when both unicells and colonial forms are included in the study. Again, there is no evidence of phyletic dependence when comparing green algae and cyanobacteria. The reason that unicells alone show a stronger allometric relationship between size and growth rate than is shown by the total data sets becomes clear when data for colonial forms alone are analysed: There is absolutely no relationship between size and maximum growth rate in either colonial green algae or colonial cyanobacteria. This is in accordance with the hypothesis (Niklas, 2000) that the colonial growth form represents an evolutionary solution to the problem that is inherent in size-dependent growth: that the growth rate decreases with increasing size. By being colonial these species can escape the constraints of size-dependent growth and achieve higher growth rates than would be possible for unicells of a similar size. They do this by becoming flatter in the sense that shape is measured as $(\text{surface area})^3 \times (\text{volume})^{-2}$ (Niklas, 1994): many colonial cyanobacteria and some colonial green algae are filamentous and as such they can increase their size without increasing the diffusional pathway from their surface to the cell interior simply by becoming longer. Other colonial algae form colonies more or less shaped as flat discs or plates still only one or a few cell layers thick, and even the largest colonial green algae among the Volvocales form colonies that are hollow spheres. Although they may be several hundred μm in diameter, they still are only one cell layer thick. Interestingly, some very large unicellular diatoms, such as Ethmodiscus, whose cell volume is dominated by the vacuole, are also able to achieve growth rates that are higher than would be predicted from their size. In this respect, they can be seen as analogues to the hollow-sphere growth form (Villareal *et al.*, 1999).

The efficiency of supply of various substances by diffusion from the cell surface as well as the capacity for light interception for various geometric shapes decrease in the order plate > cylinder > disk > sphere (Niklas and Kerchner, 1984; Niklas, 1994, 2000). It is therefore advantageous for larger photosynthetic organisms to be as flat or oblong as possible to avoid diffusional limitation at low nutrient concentrations, and the colonial life form probably gives the organisms larger flexibility regarding possible geometric shapes. Very small unicellular organisms are close to being spherical (Niklas, 2000), and although unicellular forms too become flatter with increasing size (Niklas, 2000), the fact that they consist of only one cell probably constrains not only achievable size, but also possible geometric form. Colonial algae can thus take advantage of the positive aspects of size, e.g. lower grazing pressure (Cyr and Pace, 1993), without paying the full cost of decreased metabolism and reduced growth (Niklas and Kerchner, 1984; Niklas, 1994, 2000) that is predicted from the size-dependent growth (Nielsen and Sand-Jensen, 1990; Enríquez *et al.*, 1996; Nielsen *et al.*,

1996). The colonial growth form enables exchange of metabolites among neighbours (Niklas, 2000) and it is also entirely possible that some of the colonial forms have division of labor among the cells. This has been shown to be the case in the Volvocales (Kirk, 1998), where division of labor occurs above a threshold of about 64 cells (Bell, 1985). Division of labor will give colonial forms advantages over unicells in addition to those brought about by size itself.

The data do not allow any firm conclusions as to the schism between the surface law and the Kleibers rule. The scaling exponent found for unicells are in accordance with both 'laws', but when the total datasets are considered, only Kleibers rule describes the data sufficiently. This may, however, be regarded as an artifact due to the inclusion of the colony-forming algae, that do not follow any allometric relationships between size and maximum growth rates.

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APPENDIX 1

List of species of which data are included in this study.

Cyanobacteria

Anabaena sp.
Anabaena affinis
Anabaena circinalis
Anabaena flos-aqua
Anabaena oscillatoides
Anabaena solitaria
Anabaena spiroides
Anabaena variabilis
Anacystis sp.
Aphanizomenon flos-aquae
Gloeobacter violacea
Gloeotrica echinulata
Limnotrix redekei
Merismopedia tenuissima
Microcoleus chtonoplastes
Microcystis aeriginosa
Microcystis reinboldii
Microcystis viridis
Microcystis wesenbergii
Nodularia sp.
Oscillatoria sp.
Oscillatoria agardhii
Oscillatoria bourrellyi
Oscillatoria limnetica
Oscillatoria redekei
Oscillatoria tenuis
Phormidium sp.
Phormidium autumnale
Phormidium mucicola
Phormidium tenue
Pinnularia borealis
Planktosphaerella terrestris
Planktothrix agardhii
Planktothrix rubescens
Prochlorococcus sp.
Pseudoanabaena catenata
Schizothrix calcicola
Spirulina maxima
Symploca sp.
Synechococcus sp.
Synechococcus leopolensis
Synechococcus linearis
Synechocystis sp.
Zygnema sp.

Green algae (Chlorophyta)

Ankyra sp.
Asterococcus superbus
Chlamydomonas sp.
Chlamydomonas brannonii
Chlamydomonas cribum
Chlamydomonas frankii
Chlamydomonas gigantea
Chlamydomonas gymnogama
Chlamydomonas moewsii
Chlamydomonas noctigama
Chlamydomonas pulsatilla
Chlamydomonas reinhardti
Chlamydomonas subglobosa
Chlorella sp.
Chlorella marina
Chlorella nana
Chlorella ovalis
Chlorella pyrenoidosa
Chlorella salina
Chlorella spaerchkii
Chlorella vulgaris
Chlorogonium elongatum
Choricystis coccoides
Closterium acculare
Friedmannia sp.
Gonium sociale
Heteromastix pyriformis
Hydrodictyon africanum
Lagerheimia subsalsa
Micromonas pusilla
Monoraphidium concortum
Nannochloris bacillaris
Nannochlorum eucarotum
Oocystis pusilla
Pediastrum angulosum
Pediastrum biradiatum
Pediastrum boryanum
Pediastrum duplex
Pediastrum tetras
Pleodorina californica
Prototheca zopfii
Scenedesmus abundans
Scenedesmus acuminatus
Scenedesmus armatus
Scenedesmus obliquus
Scenedesmus quadricauda
Selenastrum bibraianum
Selenastrum capricornutum
Coelastrum microporum
Cosmarium botrytis
Cosmarium depressum
Dunaliella sp.
Dunaliella primolecta
Dunaliella salina
Dunaliella tertiolecta
Eudorina elegans
Eudorina unicoccus
Sphaerellopsis aulata
Sphaeocystis sp.
Sphaerocystis achroeterii
Staurastrum luetkemuelleri
Staurastrum pingue
Stichococcus sp.
Tetraedon bitridens
Tetraedon minimum
Volvox aureus

APPENDIX 2

Sources of data on growth rates and/or cell and colony size used in this paper.

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