

Some size relationships in phytoflagellate motility

Ulrich Sommer

Max Planck Institute of Limnology, P.O. Box 165, D-2320 Plön, FRG

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Abstract

Data from the literature are used to assess some hypothesised adaptive advantages of the flagellate life form among phytoplankton. Possible advantages include increased nutrient uptake by movement through a homogeneous medium as opposed to exploitation of spatial heterogeneity of the environment. Maximal migrational amplitudes and maximal swimming velocities of phytoflagellates were compared to body size. Both were found to increase with size. Relative amplitudes and relative velocities, however, were found to decrease with size. Hydrophysical considerations show that additional gain of nutrients by swimming through a homogeneous medium is only minimal for small flagellates at their attainable swimming velocities. It is suggested that exploitation of environmental heterogeneity in nutrient distribution may be one of the most important advantages for flagellates over coccoid algae.

Introduction

In 1963 Lund published an article with the title 'A rarely recorded but very common British alga, *Rhodomonas minuta* Skuja'. Since then the importance of small flagellates in phytoplankton has become widely recognised, but reasons for their widespread success have yet to be explained. In no culture competition experiment in which flagellates were present in the inoculum, has a flagellate been a successful competitor (Smith & Kalff, 1983; Sommer, 1983; Kilham, 1986). The much greater success of flagellates in nature can probably not be explained by resistance against losses. Comparative grazing studies indicate that athecate flagellates of the size of *Rhodomonas* are more efficiently grazed by zooplankton than coccoid phytoplankton of similar size (e.g., Knisely & Geller, 1986). Only avoidance of sinking losses seems to be a major advantage for flagellates. However, this advantage should be important only in relation to diatoms, desmids, and large Chlorococcales.

One fundamental difference between experimen-

tal cultures and natural water bodies is the destruction of spatial structure in mixed cultures. In natural waters there is always a vertical gradient of light, in the case of thermal stratification also often of nutrients. Both might be exploited by vertically motile algae (photosynthesis in upper, nutrient uptake in lower strata, cf. Salonen *et al.*, 1984). Besides this classic example of spatial heterogeneity nutrient micropatchiness has recently become the focus of theoretical considerations about nutrient limitation (Goldman *et al.*, 1979). With the initial idea (excretion plumes from zooplankton) being discredited on physical ground (Jackson, 1980) organismic-detrital microaggregates ('marine snow') have now been suggested as sites of locally elevated nutrient concentrations (Goldman, 1984). Goldman argued that flagellates should encounter such aggregates more frequently than immobile algae and therefore experience an advantage.

The spatial scale of the two mentioned types of heterogeneity differ by several orders of magnitude. The ability to exploit both or the micropatchiness alone should depend on swimming velocities and

migrational amplitudes. Here I test literature data on migration amplitudes *in situ* and swimming velocities measured microscopically for trends related to size, shape or taxonomic position. Unfortunately there is a strong bias towards dinoflagellates in both data sets.

Amplitude of diel vertical migrations

Obviously flagellates do not always fully realise their potential migrational amplitudes, because profitable environmental gradients occur over shorter distances or the migrational range may be truncated by anaerobic water layers or the bottom of the lake. In order to come as close as possible to the migratory potential of the species discussed here, I have compiled the maximum values I could find in the literature for each species (Table 1). Migrational ampli-

tudes have either been taken from the original source or calculated as the maximum diel differences in the medians of depth distributions. Wherever the original authors used instead the vertical displacement of peaks, the values have been recalculated from the original profiles. If the original sources contained no size data, averages from the taxonomic literature have been taken. Size is expressed as the diameter of the spherical equivalent volume (DSE).

The scatter plot of the data shows a weak size-related trend. If the conventional allometric equation for physiological size dependencies (Peters, 1983) is fitted to the data (Fig. 1) the equation becomes $A=1.51 \cdot 10^6 \cdot \text{DSE}^{0.40}$ with a correlation coefficient of 0.61 (amplitude and DSE expressed in μm). Apparently, marine species do not differ markedly from freshwater ones. Unfortunately, there is a lack of data for small marine and for very small freshwater flagellates. If the trend is extrapo-

Table 1. Maximum recorded amplitude of diel vertical migrations (m) and size expressed as diameter of spherical equivalents (DSE, μm) of phytoflagellates.

Species	Amplitude	DSE	Source
FRESHWATER			
<i>Peridinium cinctum</i>	10	49	Berman & Rodhe, 1971
<i>Ceratium hirundinella</i>	5	46	Frempong, 1984
<i>Peridinium aciculiferum</i>	8	34	Nauwerck, 1963
<i>Gymnodinium uberrimum</i>	5.5	33	Tilzer, 1973
<i>Peridinium penardii</i>	5	31	Sibley <i>et al.</i> , 1974
<i>Gymnodinium lacustre</i>	2.5	13	Tilzer, 1973
<i>Synura petersenii</i>	2.5	53	Tilzer, 1973
<i>Mallomonas tonsurata</i>	2.8	13	Ilmavirta, 1974
<i>Mallomonas</i> sp.	7.5	8.4	Tilzer, 1973
<i>Dinobryon sertularia</i>	7.5	16	Tilzer, 1973
<i>Cryptomonas ovata</i>	5	19	Tilzer, 1973
<i>Cryptomonas erosa</i>	3	19.5	Ilmavirta, 1974
<i>Cryptomonas marssonii</i>	5.5	12	Soeder, 1967
<i>Rhodomonas minuta</i>	2.5	5.4	Sommer, 1982
<i>Rhodomonas lens</i>	4	7.8	Sommer, 1982
<i>Chroomonas acuta</i>	3	8.3	Ilmavirta, 1974
<i>Volvox</i> sp.	18	108	Sommer & Gliwicz, 1986
MARINE			
<i>Ceratium tripos</i>	10	82	Sournia, 1982
<i>Ceratium furca</i>	5	67	Blasco, 1978
<i>Gonyaulax polyedra</i>	14	58	Blasco, 1978
<i>Ceratium fusus</i>	10	50	Hasle, 1950
<i>Prorocentrum mariae-lebouriae</i>	6	42	Sournia, 1982
<i>Prorocentrum micans</i>	6	27	Hasle, 1950

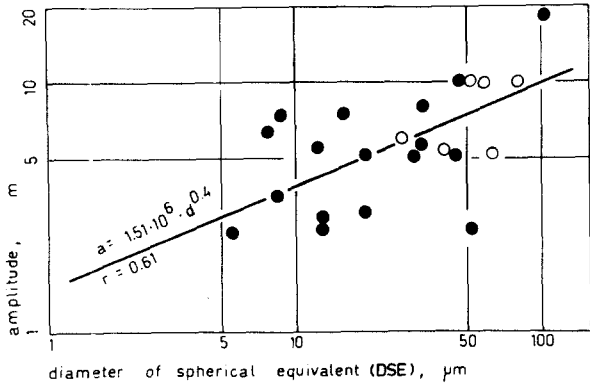


Fig. 1. Dependence of amplitude of vertical migration in on size expressed as diameter of spherical equivalent (DSE) for fresh-water (●) and marine (○) flagellates. The regression line is for the full data set.

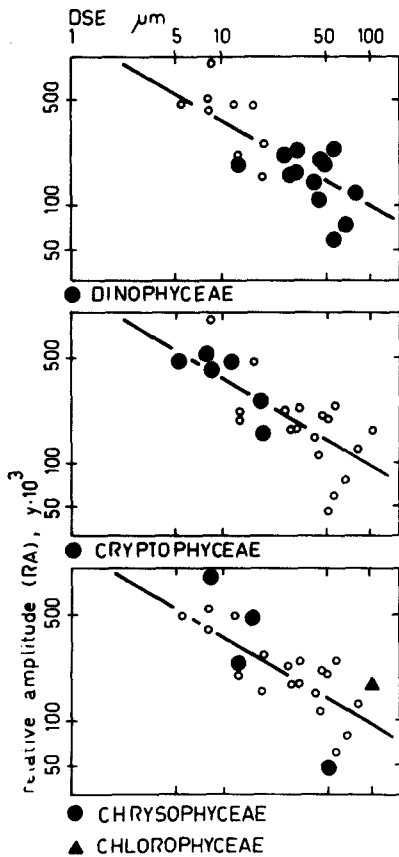


Fig. 2. Relationships between relative migration amplitude (RA) and size expressed as diameter of spherical equivalent (DSE) for several higher taxa of phytoflagellates. In all cases the fitted regression line is that for the full data set data set ($RA = 1.51 \cdot 10^6 \cdot DSE^{-0.6}$).

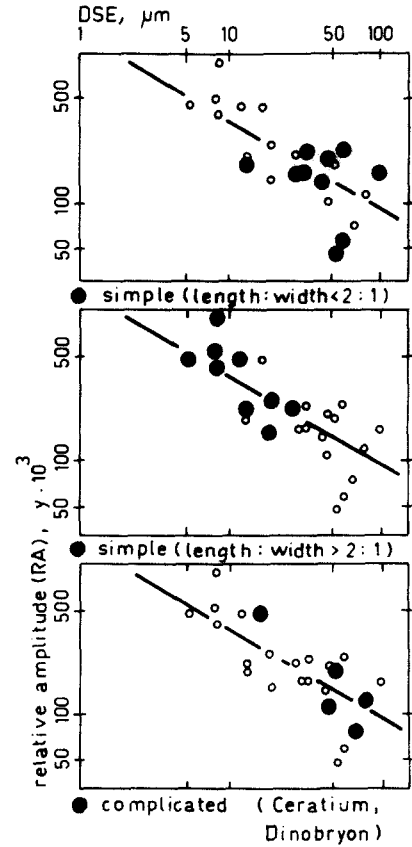


Fig. 3. Relationships between relative migration amplitude (RA) and size expressed as diameter of spherical equivalent (DSE) for different shape types of phytoflagellates. In all cases the fitted regression line is that for the full data set ($RA = 1.51 \cdot 10^6 \cdot DSE^{-0.6}$).

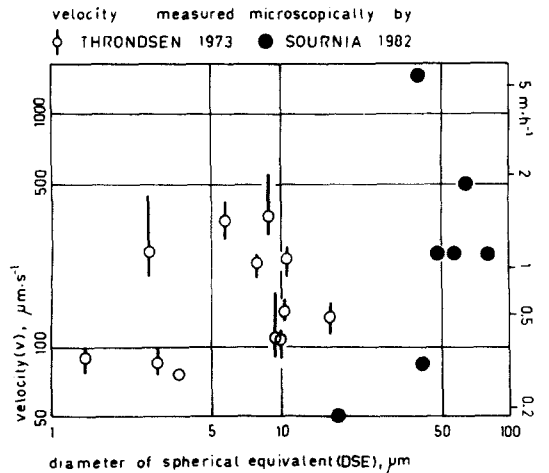


Fig. 4. Swimming velocity (v) of marine flagellates in relation to size expressed as diameter of spherical equivalent (DSE).

lated to very small flagellates (less than 5 μm) it seems that vertical migration would be profitable for them only in water bodies with steep environmental gradients, where relevant differences occur at a vertical distance of less than about 2 m.

If the amplitudes are converted into relative amplitudes ($RA = \text{amplitude}/\text{size}$) an inverse size-related trend becomes obvious: $RA = 1.51 \cdot 10^6 \cdot DSE^{-0.60}$ ($r = -0.75$). A grouping of data by higher taxa (classes) shows no marked taxonomic deviations from the general trend (Fig. 2). However, this conclusion must be considered preliminary, since all

classes except dinoflagellates are represented by too few examples. A similar preliminary conclusion must be drawn for shape types (Fig. 3) if flagellates are split into stout simple shapes (spherical or ovoid/elliptic with a length:width ratio of less than 2:1), elongate simple shapes (length:width more than 2:1), and complicated shapes (here only *Ceratium* and *Dinobryon*).

Swimming velocities

The comparison of swimming velocities (Table 2) re-

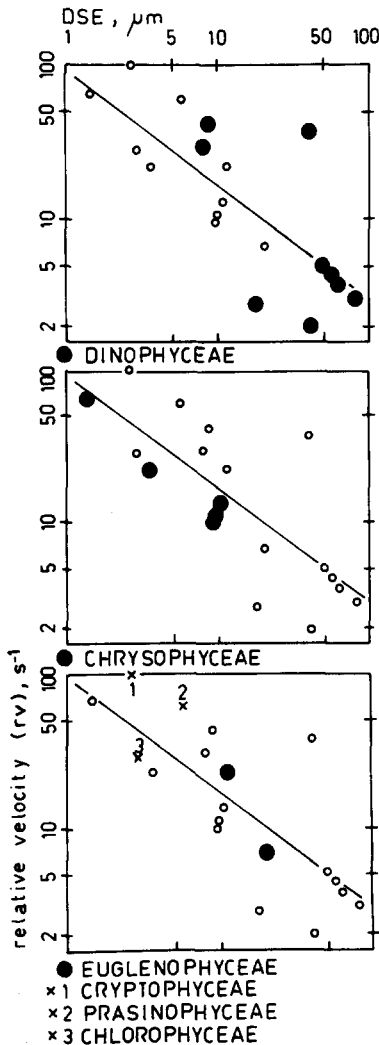


Fig. 5. Relationships between relative swimming velocity (rv) and size expressed as diameter of spherical equivalent (DSE) for several higher taxa of marine flagellates. In all cases the fitted regression line is that for the full data set ($rv = 93 \cdot DSE^{-0.76}$).

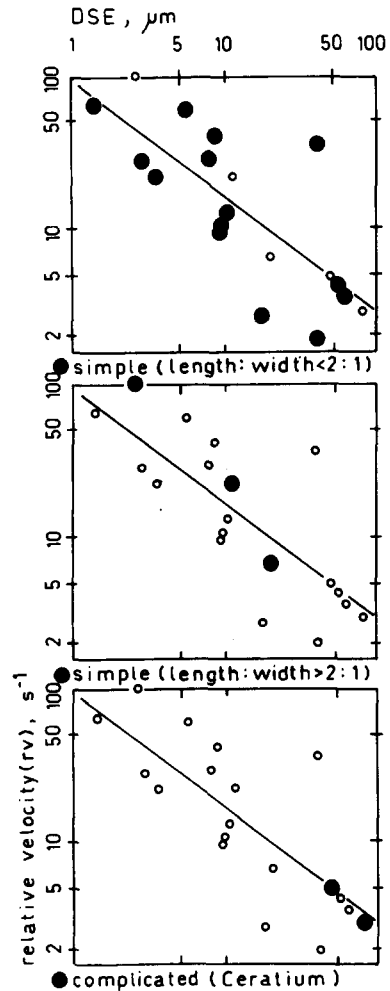


Fig. 6. Relationships between relative swimming velocities (rv) and size expressed as diameter of spherical equivalent (DSE) for different shape types of marine flagellates. In all cases the fitted regression line is that for the data set ($rv = 93 \cdot DSE^{-0.76}$).

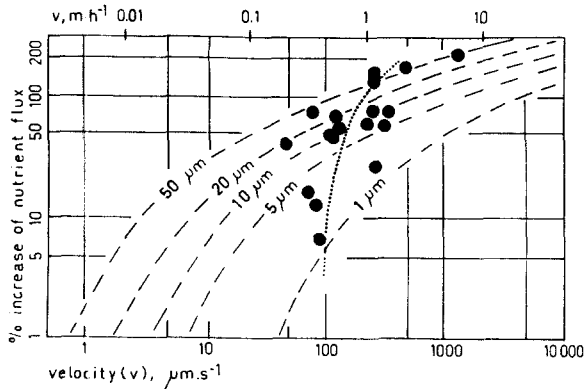


Fig. 7. Fractional increase of nutrient flux to the cell surface as a function of swimming velocity and diameter, calculated for spherical cells (after Berg & Purcell, 1977). The full circles represent that data points from Table 2 and the dotted line is the regression of swimming velocity on cell size ($v = 93 \cdot \text{DSE}^{0.24}$).

lies on two data sets: Throndsen (1973) and Table 2 in Sournia (1982) which is a compilation of data from several authors. Both sources comprise only data for marine species. Fig. 4 shows only a weak size-related trend of swimming velocities ($v = 93 \cdot \text{DSE}^{0.26}$; $r = 0.38$; v in $\mu\text{m} \cdot \text{s}^{-1}$). Logically,

Table 2. Swimming velocity ($\mu\text{m} \cdot \text{s}^{-1}$) and size (diameter of spherical equivalent, μm) of marine flagellates (data from Throndsen, 1973 and Sournia, 1982).

Species	DSE	v
<i>Ceratium tripos</i>	82	250
<i>Dinophysis acuta</i>	66	500
<i>Gonyaulax polyedra</i>	58	250
<i>Ceratium fusus</i>	50	250
<i>Proocentrum mariae-lebouriae</i>	42	83
<i>Protoperdinium quinquecorne</i>	40	1500
<i>Eutreptiella</i> sp.	20	135 (115–155)
<i>Heterocapsa</i> sp.	18	50
<i>Eutreptiella gymnastica</i>	11	240 (200–275)
<i>Olisthodiscus luteus</i>	10.5	140 (130–160)
<i>Pseudopedinella pyriformis</i>	9.8	105 (90–110)
<i>Apedinella spinifera</i>	9.5	110 (90–175)
<i>Katodinium rotundatum</i>	8.8	370 (300–550)
<i>Gyrodinium</i> sp.	7.8	230 (200–245)
<i>Pyramimonas disomata</i>	5.8	350 (290–420)
<i>Ochromonas minima</i>	3.6	75
<i>Heteromastix pyriformis</i>	3	85 (75–100)
<i>Hemiselmis simplex</i>	2.6	260 (200–450)
<i>Micromonas pusilla</i>	1.4	90 (75–100)

the slow rise of swimming velocities with size implies a sharp decrease of relative velocities ($RV = \text{velocity}/\text{size}$) with size ($rv = 93 \cdot \text{DSE}^{-0.74}$; $r = -0.76$).

The data available so far do not indicate any taxonomic trend apart from the general size-related trend (Fig. 5), although for most taxa data are still too few. A similar conclusion must be drawn for shape types (Fig. 6).

Discussion

It has been argued that motion relative to the surrounding water should be advantageous even in an homogeneous environment (Munk & Riley, 1952; Margalef, 1978). By moving, organisms would escape from nutrient-depleted diffusion shells around the cells and be 'washed' by fresh medium. Gavis (1976), Berg and Purcell (1977) and Purcell (1977) have examined these arguments for particles with the low Reynolds numbers characteristic for phytoplankton. There is a zone of shear around the cell, the extent of which is dependent on size, swimming velocity and viscosity of the medium. This local fluid environment is partially carried along with the swimming cell. The nutrient flux to cell surface improves with increasing size and with increasing velocity. As can be seen in Fig. 7, a small flagellate would need the impossible swimming velocity of $5000 \mu\text{m} \cdot \text{s}^{-1}$ to increase the nutrient flux by 100%; realistic swimming velocities would increase the nutrient flux only by 5 to 20%. For $5 \mu\text{m}$ flagellates, however, an increase by about 50% should be possible; for still larger flagellates increases up to 200% become possible. Goldman (1984) concluded from such data that swimming in a homogeneous medium is not significantly advantageous for very small flagellates. By developing his argument further he derived support for his marine snow hypothesis from the predominance of small flagellates in oceanic phytoplankton. It might be argued, however, that a 5 to 20% gain in nutrient uptake is by no means a zero advantage. Metabolic costs of flagellar movements have been calculated to be extremely low. Raven & Richardson (1984) calculated costs of $1.13 \cdot 10^{13} \text{W} \cdot \text{cell}^{-1}$, which translates to

0.725 W · kg⁻¹ biomass for their model dinoflagellate. This is 240000th part of the minimum power consumption in growth at a generation time of 24 h. Purcell (1977) calculated a very similar figure (0.5W · kg⁻¹) for the swimming costs of the motile bacterium *Escherichia coli*, which should be comparable to small algal flagellates. If the costs of swimming are really this marginal, then clearly also the gains from swimming do not have to be high in order to make swimming profitable.

Will the smallest flagellates also be able to exploit vertical gradients? If extrapolated to smaller sizes, the relationship between migrational amplitudes and size suggests that flagellates of less than 5 μm size will profit from vertical migration only if sufficient environmental differences occur at vertical distances of less than 2 m. This is to be expected in water bodies of low transparency and sufficient thermal stability. This could be tested by comparing the migration behaviour of such small flagellates in highly transparent waters and in waters of low transparency.

A further field for future investigations, where little has been done with respect to autotrophic flagellates, is the question of chemotaxis. Chemotaxis would greatly increase the possibility to exploit nutrient micropatchiness in comparison to random swimming. Sjöblad *et al.* (1978) demonstrated attraction of *Dunaliella tertiolecta* to point sources of NH₄ and several amino acids, but not to NO₃, urea and some other amino acids. Further examples are still lacking.

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