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Sinking properties of some phytoplankton shapes and the relation of form resistance to morphological diversity of plankton – an experimental study

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Abstract

Form resistance (Φ) is a dimensionless number expressing how much slower or faster a particle of any form sinks in a fluid medium than the sphere of equivalent volume. Form resistance factors of PVC models of phytoplankton sinking in glycerin were measured in a large aquarium ($0.6 \times 0.6 \times 0.95$ m). For cylindrical forms, a positive relationship was found between Φ and length/width ratio. Coiling decreased Φ in filamentous forms. Form resistance of *Asterionella* colonies increased from single cells up to 6-celled colonies than remained nearly constant. For *Fragilaria crotonensis* chains, no such upper limit to Φ was observed in chains of up to 20 cells (longer ones were not measured). The effect of symmetry on Φ was tested in 1–6-celled *Asterionella* colonies, having variable angles between the cells, and in *Tetrastrum staurogeniaeforme* coenobia, having different spine arrangements. In all cases, symmetric forms had considerably higher form resistance than asymmetric ones. However, for *Pediastrum* coenobia with symmetric/asymmetric fenestration, no difference was observed with respect to symmetry. Increasing number and length of spines on *Tetrastrum* coenobia substantially increased Φ. For a series of *Staurastrum* forms, a significant positive correlation was found between arm-length/cell-width ratio and Φ: protuberances increased form resistance. Flagellates (*Rhodomonas, Gymnodinium*) had a $\Phi < 1$: they sank faster than the spheres of equivalent volume. *Ceratium* ($\Phi = 1.61$) proved an exception among flagellates: in most forms tested in this study (ellipsoid flagellates, *Staurastrum* forms with no or very short protuberances, and *Cosmarium* forms), $\Phi > 1$. The highest value ($\Phi = 8.1$) was established for a 20-celled *Fragilaria crotonensis* chain. Possible origin of the so-called 'vital component' (a factor that shows how much slower viable populations sink than morphologically similar senescent or dead ones) is discussed, as is the role of form resistance in evolution of high diversity of plankton morphologies.

Introduction

After Antoni van Leeuwenhoek (1632–1723) constructed his first microscopes, morphological variability, diversity and the general *beauty* of planktonic organisms have attracted generations of taxonomists and plankton ecologists. The huge diversity that we can see under the microscope evolved during the millennia of life on planet Earth and the main evolutionary driving force was certainly something other than to fascinate scientists.

Planktonic organisms are usually small and they have short generation times. Typical temporal patterns include irregular fluctuations around a more or less constant level, increases and decreases over long periods, cyclic oscillations and occasionally explosive bursts by populations normally existing at low levels (Lampert & Sommer, 1997). The net growth rate (r) of a phytoplankton population can be expressed as $r = \mu - \lambda$, where μ is the gross growth rate and λ symbolizes losses. The latter, λ, includes various sources of loss, such as predation (grazing by the zooplankton), physiological mortality due to aging, the mortality caused by parasites, washout loss to the outflow and settlement to the bottom sediments. These loss factors are rather universal for most biota, except washout and sedimentation are quite specific for plankton. The velocity of a particle sinking in a fluid medium can be described by the Stokes equation:

$$v_s = \frac{2gr^2(p' - p)}{g\eta\Phi},$$

where v_s [m s^{-1}] is the sinking velocity, $\boldsymbol{g}$ [m s^{-2}] is the gravitational acceleration, r [m] is the radius of the sinking spherical particle, p' is the specific gravity of the sinking particle [kg m^{-3}], p is the specific gravity of the fluid medium [kg m^{-3}], and η [kg m^{-1} s^{-1}] is the viscosity of the medium. Φ is the form resistance factor, which is a dimension-less number and it expresses the factor by which the sinking velocity of the particle differs from that of a sphere of identical volume and density. If a planktonic species evolves towards minimizing its sinking losses, it has three options: it may decrease its body size (however, to do so is to increase the risk of being grazed by zooplankton), it may decrease its specific gravity (examples include gas vacuoles of cyanoprokaryota and the accumulation of oil-droplets as storage product), or it may increase its form resistance.

The validity of the Stokes equation was tested in experiments with simple geometrical forms made of metal and sinking in viscous oil. It was shown that each shape tested, except the tear-drop, sank more slowly than the equivalent sphere (McNown & Malaika, 1950). For phytoplankton species generally, form resistance factors between 0.94 and 5.49 were established (Reynolds, 1984). The method of most experiments aiming establishment of Φ was measuring sinking velocity of a laboratory culture of a given species and comparison of the measured values to those estimated from the Stokes-equation for spheres.

The aim of the present study was to measure form resistance of the most common phytoplankton forms and/or morphological types, using artificial PVC models of algal forms in a laboratory experimental aquarium containing a viscous fluid.

Experimental design, material and method

Two basic criteria were kept in mind when designing the experimental aquaria to study sinking velocities. (i) Sinking particles generate turbulence as they move through water, whereas the influence of turbulence on sinking velocities needed to be excluded. Therefore, the experimental aquarium had to be both wide (to avoid wall-effects) and long (to allow as long way to sink as possible for enhancing accuracy of the measurements). (ii) As the density difference between water (max. 1 g cm^{-3}) and phytoplankton is rather small (the heaviest diatoms have densities up to 1.29 g cm^{-3}; for other groups than diatoms the 1.04 g cm^{-3} is characteristic [Reynolds, 1984]), we needed to minimize the density difference between the medium and sinking particles.

The experimental system consisted of two aquaria. The inner was 0.6 × 0.6 × 0.95 m and the outer was 0.7 × 0.7 × 0.95 m (vertical dimensions were the highest; thickness of the glass was 1.0 cm). Since the densities of most fluid media are highly temperature-dependent, the outer aquarium was intended to moderate the inner one. However, this precaution proved to be unnecessary since the experiments themselves could be carried out rapidly (even with many repetitions) and it proved to be easier to establish calibration curves for any given ambient temperature than to operate a heating system (+ stirring pumps) in the external aquarium. A simple mosquito net fixed on an iron-frame was placed at the bottom of the aquarium for recovering settled particles.

Concerning the medium and the material for the artificial algae, the mineral oil + clay ceramics seemed initially to be an optimal combination but we were compelled to reject it. Most mineral oils that were sufficiently viscous were not adequately transparent, so requiring the installation of electronic sensors to record settlement times. Moreover, it seemed both problematic and unappealing to recover particles from the bottom of the aquarium prior to making replicate measurements with the same particle. For these reasons, we decided to use glycerine as the fluid medium (86.5%, P 20–25 °C = 1.2271 – 1.2214 g cm^{-3}; Perry, 1969).

For the model algae used in the first set of experiments, we used PVC-U (P' = 1.37 g cm^{-3}). This material is a hard plastic and ideal for machine turning. Thus, the density difference between the sinking particle and the medium was $\sim$ 1.12 which falls into the range of the density difference between algae and water. Algal shapes (spheres, rods, *Astrionella formosa* and *Fragilaria crotonensis*) were machine-turned and used for the experiments. Later, we had to accept that machine turning, although capable of producing near-identical ‘cells’, is not appropriate for fashioning the complex forms of *Staurastrum* or *Ceratium*. For making such forms, a PVC-based (Plastillin-like) modeling material (HAVO B.V. POB 320, 3850 AH Ermelo, Holland) was used. This material is com-

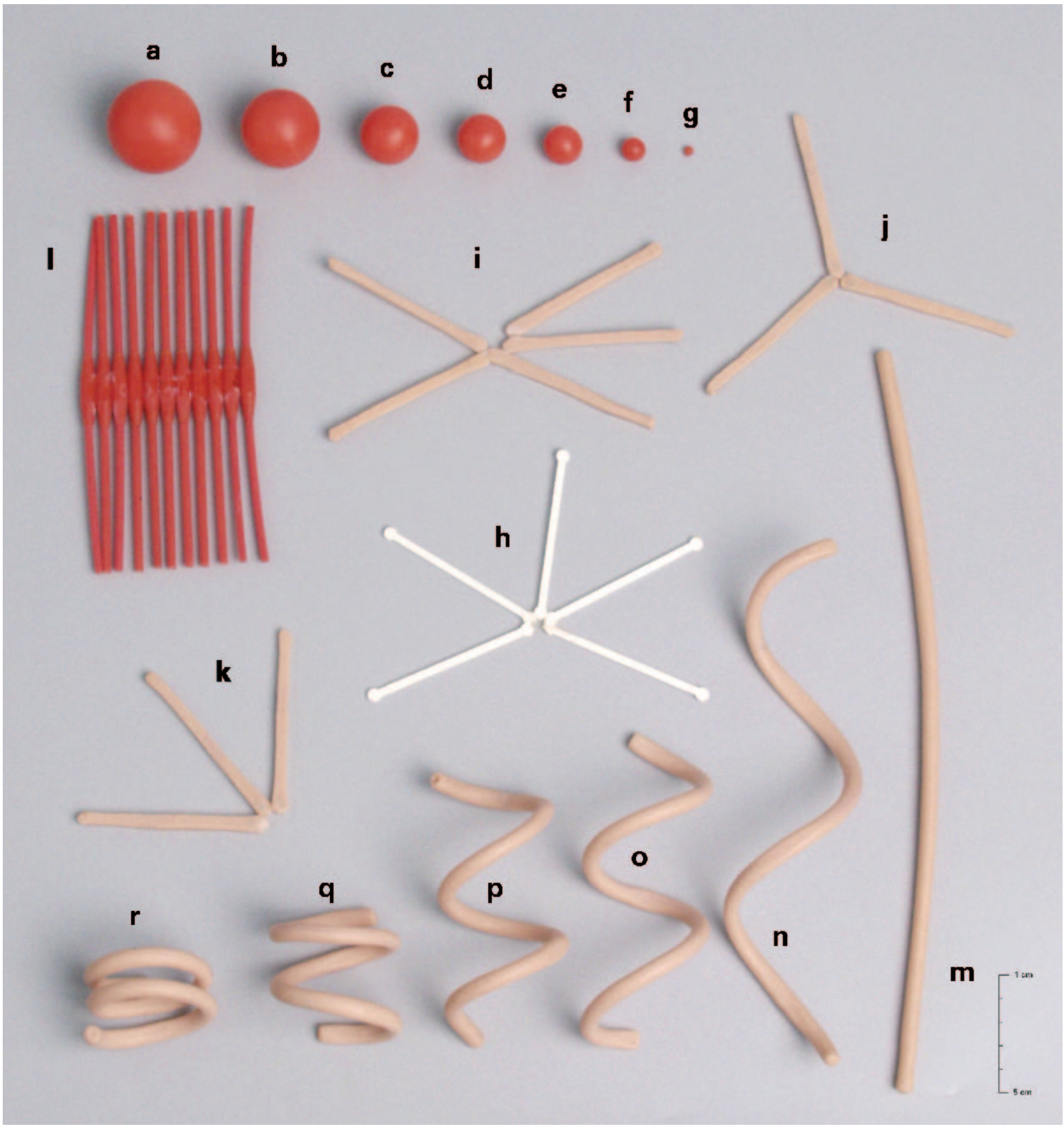

Plate I. (a–g) example of series of spheres used for calibration; (h–i) *Asterionella* colonies with 5 cells and diifferent symmetry; (j) symmetric *Asterionella* colony with 3 cells; (k) asymmetric *Asterionella* colony with 3 cells; (l) *Fragilaria crotonensis* chain with 11 cells; m–r: filaments coiled at different degree. Forms a–h and l were made of PVC-U, the others of modelling material. Scale bar spans 5 cm.

monly found in toy- or hobby-shops; target users are children who make flowers, animals, etc. from it because it is readily malleable. Then they can be put into kitchen-oven where they harden (without losing its original bright colors). In our experiments, algal shapes were heat-treated (130 °C) in a kitchen oven for 30 min. The specific gravity of this material was established as 1.84 g cm^{-3} so that its density ratio to glycerine is 1.50. This is higher than the ratio between phytoplankton and lake water, however, we had to compromise. Spines for *Tetrastrum*-like forms were cut from thin but hard transparent plastic and were glued onto the forms. Photographs of some artificial algae are provided on Plates I–III.

Sinking times of each particle were measured in many replicates and the averages were used for the

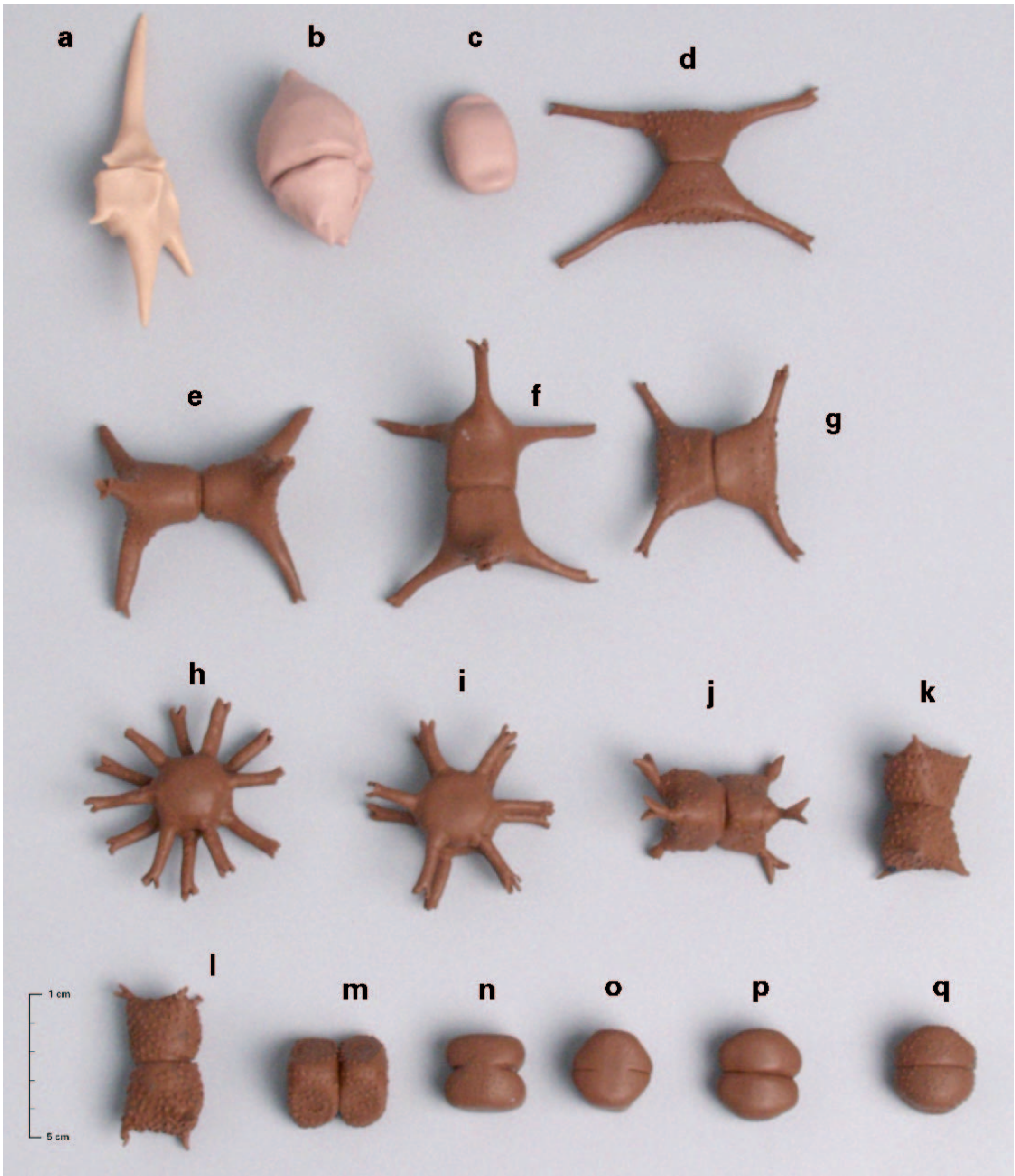

Plate II. (a) *Ceratium hirundinella*; (b) *Gymnodinium helveticum*; (c) *Rhodomonas lens*; (d) *Staurastrum chaetoceras*; (e) *Staurastrum planktonicum*; (f) *Staurastrum luetkemuellerii*; (g) *Staurastrum tetracerum*; (h) *Staurastrum rotula* with alternating protuberances (natural form); *Staurastrum rotula* with ovalapping protuberances (artificial form); (j) *Staurastrum pelagicum*; (k) *Staurastrm lunatum*; (l) *Staurastrum avicula*; (m) *Staurastrum erasum*; (n) *Cosmarium bioculatum*; (o) *Cosmarium laeve*; (p) *Cosmarium ornatum* with smooth surface (artificial form); (q) *Cosmarium ornatum* with papillate surface (natural form). Each form was made of modelling material. Scale bar spans 5 cm.

further calculations. Standard deviation of sinking velocities were usually moderate.

The volumes of the algal models were measured gravimetrically and the equivalent spherical diameters were calculated. Spheres ($\Phi = 1$) of these diameters were made using the same modeling materials (PVC-U and modeling material; Plate I: a–g). These were weighed (precision: 10^{-3} g) and the diameters of non-

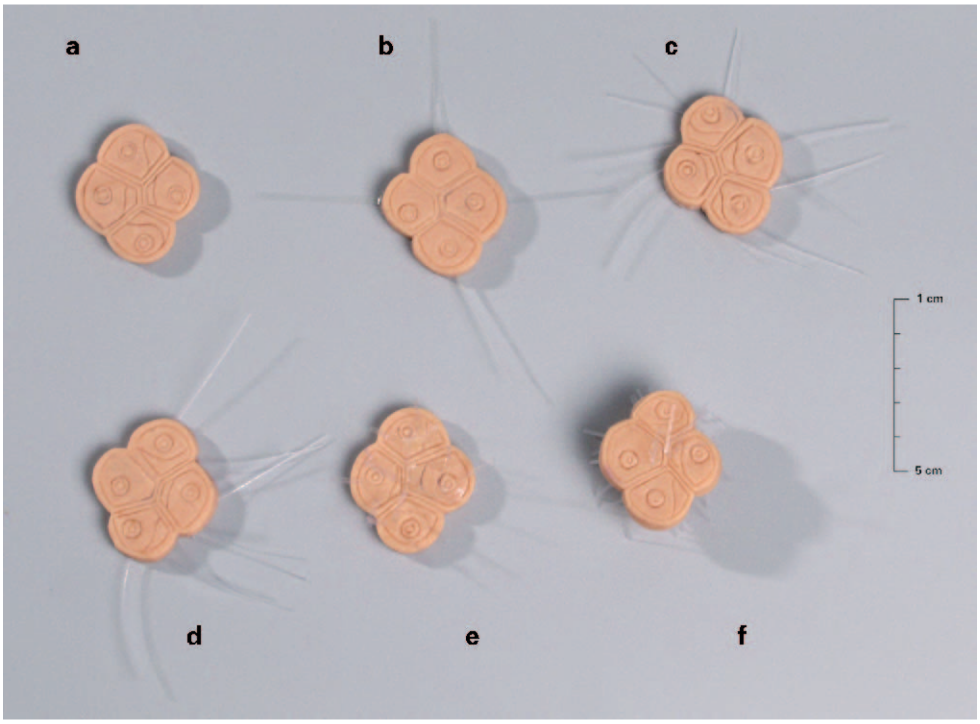

Plate III. Tetrastrum forms. (a) *T. glabrum* (no spines); (b) *T. hastiferum* with 4 symmetrically arranges spines; (c) *T. staurogeniaeforme* with ± symmetrically arranges spines; (d) *T. staurogeniaeforme* with asymmetrically arranges spines; (e–f) *T. hortobagyi* like form with different number of short, asymmetrically arranges spines. Each form was made of modelling material. Scale bar spans 5 cm.

machined spheres were verified with calipers (having an accuracy of 10^{-1} mm). From these data, mass-diameter calibration curves were obtained (Fig. 1A). Sinking velocities of each sphere were then measured and data were expressed as function of their diameter (Fig. 1B).

The estimation of sinking velocity of the spheres equivalent to given algae having a more sophisticated form was carried out on the following way: We weighed the alga (arrow 1 on Fig. 1); projected the weight-to-diameter using the relationships given in Figure 1A (arrow 2 on Fig. 1). This diameter was transferred to diameter-sinking velocity relationship given in Figure 1B (arrow 3 on Fig. 1) and then was projected to the y axis (sinking velocity) of the curves like on Figure 1B (arrow 4 on Fig. 1). Such calibration curves were established for both materials (PVC-U and modeling material) and for each series of experimental measurements. The reason for this was not only to overcome the non-standardized temperature of the glycerin, for we had also to allow for the fact that glycerin is a hygroscopic material that is liable to alter its density and viscosity through time and, so, to uncontrolled experimental conditions.

Form resistance factors were then derived from dividing the estimated sinking velocity of the volume-equivalent sphere by the sinking velocity of the corresponding form actually measured.

Results

Cylinders

These experiments were carried out with PVC-U turned forms having a standard diameter of 5 mm and lengths varying between 1 and 40 mm. Their form is expressed as length/diameter (L/D) ratio, which ranged from 0.2 to 8. Experiments with these disc- (length < diameter) or rod-like (length > to >> diameter) shapes resulted in a significant relationship ($r = 0.79$; $n = 24$; $P < 0.1\%$) between L/D and Φ (Fig. 2A). However, at L/D < 2, the two variables appeared quite independent. The apparent scattering of data (Fig. 2A) was attributable to differences in sinking position. Cylinders did not change their sinking position while sinking. Those which were started in horizontal position sank more slowly than those

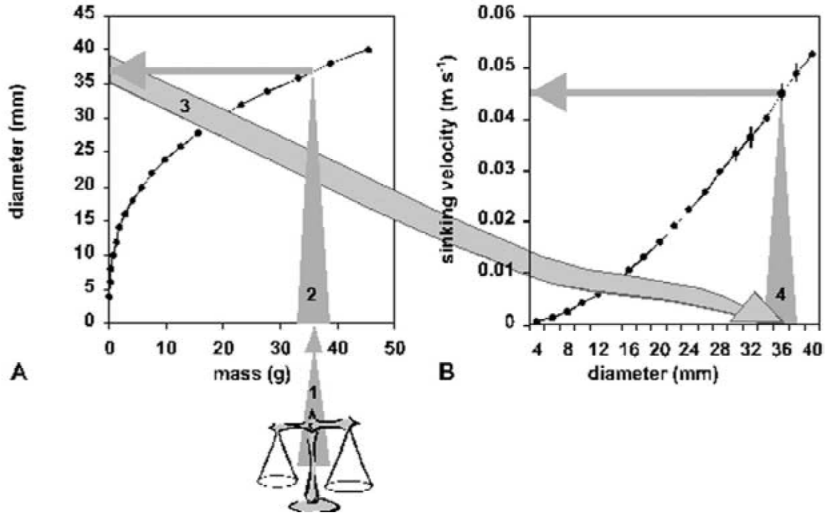

Figure 1. An example of mass-diameter (A) and diameter-sinking velocity (B) relationships for spherical particles. Grey arrows explain how sinking velocity of the sphere equivalent to a complicated form was established. First the complicated form was weighted (arrow 1), then the diameter of the equivalent sphere was calculated using relationship shown on Figure 1A (arrow 1). This diameter was transformed to Figure 1B (arrow 3) where from we got the appropriate sinking velocity (arrow 4).

set transversally and much more slowly than those set vertically. For reasons explained in the discussion, the effect of sinking position was not investigated in detail.

Effect of colony size on Φ: Fragilaria crotonensis, Asterionella

Asterionella (PVC-U forms; Plate I: h) colonies increased their Φ sharply in the range of 1 to 6 cells. Then Φ remained rather constant or even decreased slightly (Fig. 2B; records on this graph represent averages of altogether 154 individual measurements). It was apparent from the experiments that regular (8-celled) or close to regular colonies had the highest Φ. Up to 8-celled colonies, Φ of *Fragilaria crotonensis* (PVC-U forms; Plate I: l) were high but rather constant (Φ = 4.4–5.2; Fig. 2C; the number of individual measurements for this experiment was 180). For *Fragilaria* colonies consisting >8 cells, Φ increased rapidly with increasing cell numbers in the size range that was investigated (size of the aquarium did not allow construction of longer chains) reaching the highest Φ (8.1) that was recorded in any of our experiments.

Effect of coiling on Φ

For these experiments, 6 models (modeling material; Plate I: m–r) were used having exactly the same weights (volumes) and their 'straight' length was uniformly 295 mm. One of them remained slightly curved only, and the others were coiled to a differing degree. Coil width was 32 mm. For comparisons, L/D values were used where D was the width of the coil (32 mm) and length was the distance between the two ends of the filament. Similarly, as in the case of cylinders, starting position of the forms had a significant effect on Φ, however, in each case, the straightest filament had the greatest Φ and the most tightly coiled had the least (Fig. 2D).

Effect of symmety on Φ: Asterionella, Pediastrum, Tetrastrum staurogeniaeforme

When experimenting with PVC-U made *Asterionella* colonies with different cell numbers, we observed that Φ of (say) a 3-celled colony can be significantly influenced by the symmetry of arrangement of the three cells. Organisms used to test the effect of differing symmetry were *Asterionella* colonies consisting of 2–6 cells, *Pediastrum boryanum, Pediastrum duplex* and *Tetrastrum staurogeniaeforme*.

For *Asterionella* colonies, we expressed the degree of asymmetry as cumulative deviation from perfect symmetry (Plate I: i–k). For example: a 3-celled *Asterionella* colony is perfectly symmetric if each angle between the cells are 120°. For such an organism the cumulative deviation from perfect symmetry is 0 because $|(120° - 120°)| + |(120° - 120°)| + |(120° - 120°)| = 0°$. If we have a 3-celled colony where the angles

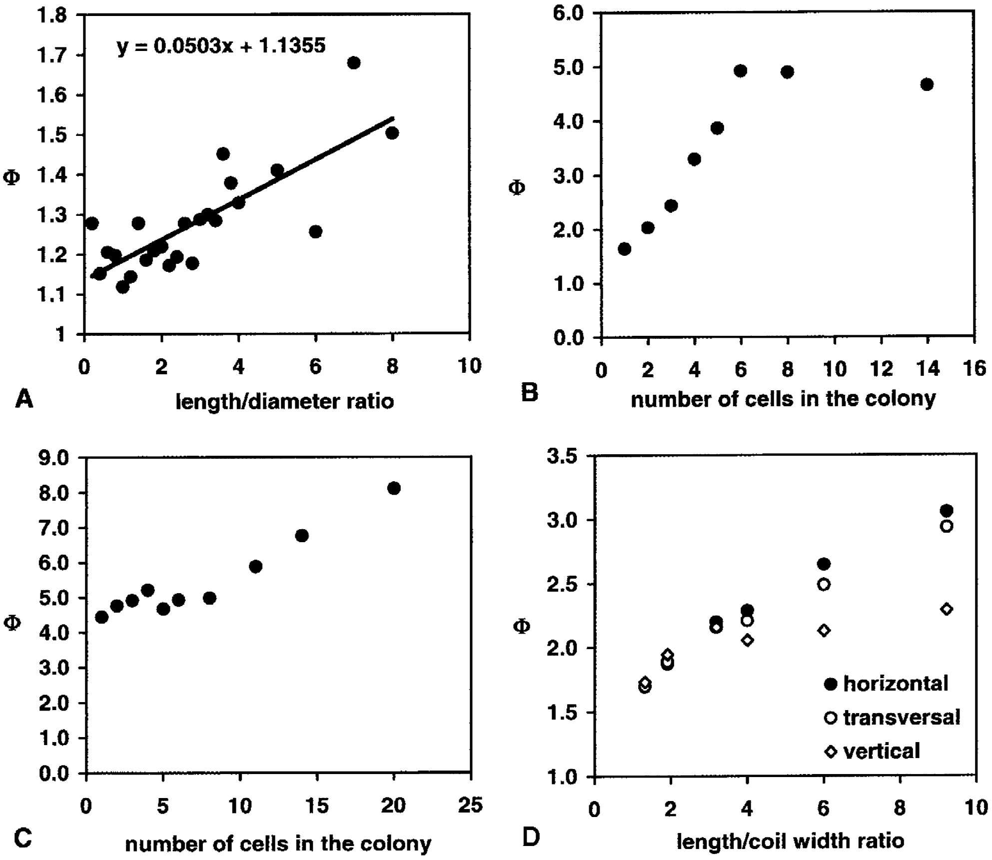

Figure 2. (A) Dependence of the form resistance factor (Φ) on the length/diameter ratio of cylindrical shapes (PVC-U). (B) Changes of the form resistance factor (Φ) depending on the number of cells in *Asterionella* colonies (PVC-U). (C) Changes of the form resistance factor (Φ) depending on the number of cells in *Fragilaria crotonensis* chains (PVC-U) and D: Changes of the form resistance factor (Φ) depending on degree of coiling expressed as length/coil width ratio (modelling material).

between the cells are 70°, 130° and 160° then the cumulative deviation from perfect symmetry can be calculated as $|(70° - 120°)| + |(130° - 120°)| + |(160° - 120°)| = 100°$. Perfect symmetry for the tested colony sizes were: 2-celled – 180°; 3-celled – 120°; 4-celled – 90°, 5-celled – 72° and 6-celled – 60°. For each case in this experiment, form resistance decreased with decreasing symmetry of the tested colonies (Fig. 3), especially for colonies comprising only 2 – 5 cells. For colonies with >5 cells the relationship became increasingly neutral.

Pediastrum coenobia (especially *P. duplex*) have a number of holes (fenestrations) among the cells forming the coenobial disc. The arrangement of cells and fenestrations is usually quite symmetric, however deviations are common in nature. Asymmetry was introduced to *Pediastrum* forms by distributing holes symmetrically or highly asymmetrically on the two halves of the coenobium, but the proportion of the area fenestrated was kept constant. Form resistance in *Pediastrum* coenobia was ~2 (Table 1) and we could not get any statistically significant relationship between degree of asymmetry imposed by hole arrangement and Φ. For this reason data are not shown. Interestingly, even highly asymmetric forms maintained their initial sinking position despite considerable weight anomalies of the two opposing halves of the coenobia.

Tetrastrum coenobia (Plate III) with asymmetrically arranged spines (Fig. 4, open circles) had lower Φ than other coenobia having the same number/size of spines but with a symmetric arrangement (neighboring forms with close circles). These asymmetric forms had even smaller Φ than forms with no spines (form nr. 1 on Fig. 4). An interesting observation on very asymmetric *Tetrastrum* cells was that, regardless of the starting position, these forms reached a final orienta-

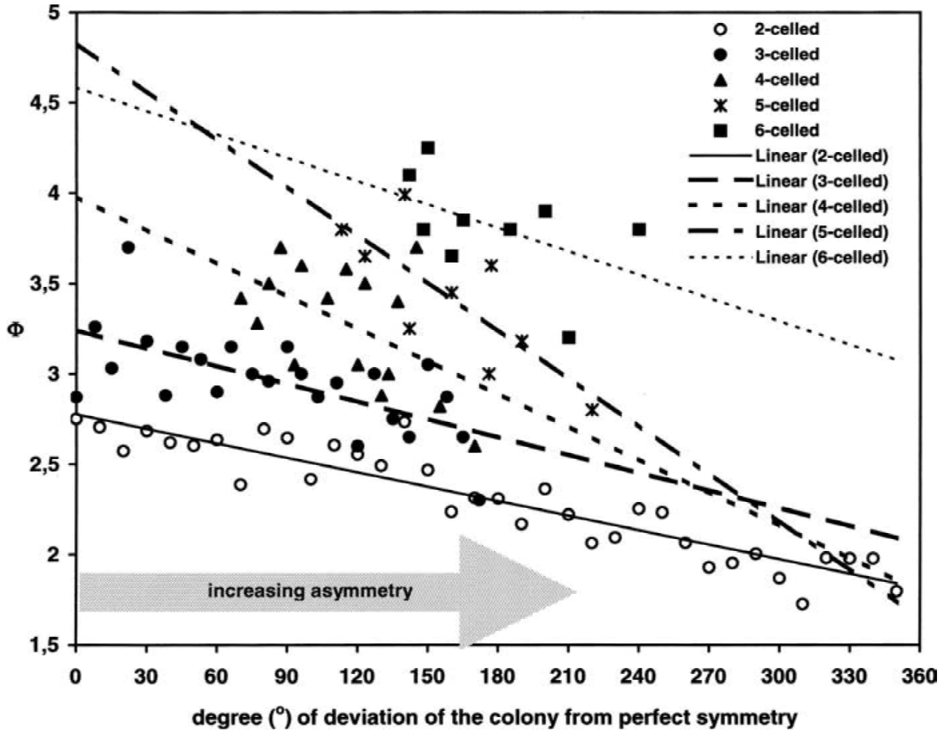

Figure 3. Changes of the form resistance factor (Φ) with increasing asymmetry (measured as cumulative degree (°) of deviation of the colony for perfect symmetry for 2-, 3-, 4-, 5- and 6-celled *Asterionella* colonies (modelling material). Trendlines according to linear regression are also indicated on the figure.

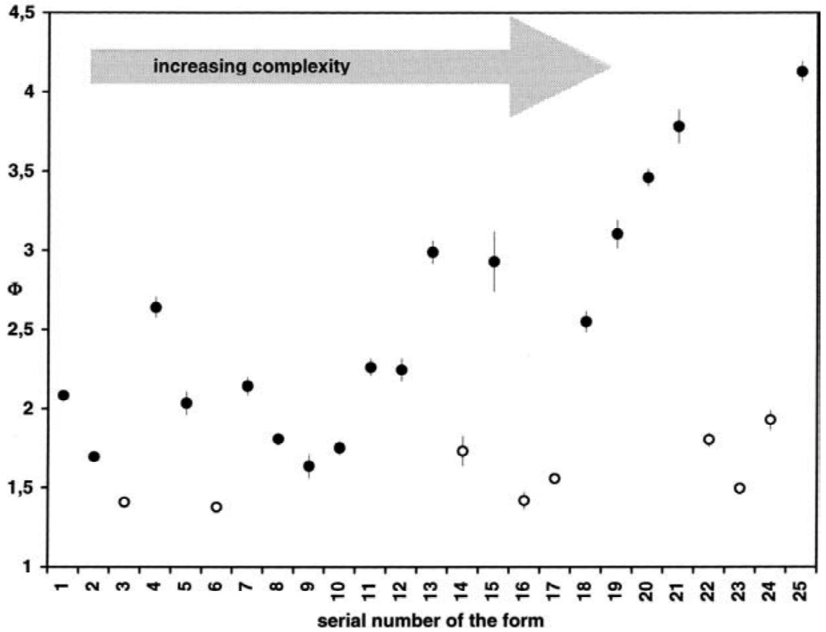

Figure 4. Changes of the form resistance factor (Φ) with increasing complexity. Serial number of modelling material made *Tetrastrum* forms are given on the x axis and they are arranged according to their increasing complexity concerning both numbers and length of attached plastic spines. Open circles represent forms with highly asymmetric arrangement of spines.

Table 1. Form resistance factor (Φ) and its standard deviation (SD) of some algal forms (modelling material)

Species	F	SD	Note
Pediastrum duplex	2.008	0.035	Horizontal sinking position
Pediastrum duplex	1.852	0.110	Vertical sinking position
Pediastrum duplex	1.936	0.037	Transversal sinking position
Pediastrum boryanum	1.908	0.041	Horizontal sinking position
Pediastrum boryanum	1.785	0.076	Vertical sinking position
Pediastrum boryanum	1.878	0.053	Transversal sinking position
Staurastrum rotula	1.424	0.027	Protuberances overlap; artificial form
Staurastrum rotula	1.459	0.019	Protuberances alternate; natural form
Staurastrum arctiscon	1.427	0.013	
Staurastrum planctonicum	1.578	0.321	
Staurastrum luetkemuelleri	1.487	0.026	
Staurastrum tetracerum	1.338	0.024	
Staurastrum chaetoceros	1.661	0.016	
Staurastrum avicula	1.058	0.018	
Staurastrum pelagicum	1.137	0.024	
Staurastrum lunatum	1.046	0.020	
Staurastrum erasum	0.886	0.018	
Cosmarium ornatum	0.837	0.003	With smooth surface
Cosmarium ornatum	0.856	0.009	With papillate surface
Cosmarium bioculatum	0.838	0.009	
Cosmarium laeve	0.810	0.005	
Ceratium hirundinella	1.609	0.170	
Rhodomonas lacustris	0.773	0.006	
Rhodomonas lens	0.676	0.004	
Gymnodinium helveticum	0.476	0.006	

tion very quickly (within the first 10 cm of sinking): with the spines on the upper side of the coenobium, dragged like a parachute.

The effect of spines (presence/absence, numbers, length, arrangement) on Φ: Tetrastrum*, desmids*

For these experiments, forms corresponding to morphologies of *Tetrastrum glabrum* (no spines; Plate III: a), *T. hastiferum* (few spines of different length; Plate III: b), *T. staurogeniaeforme* (Plate III: c,d) and *T. hortobagyi* (many spines with varying numbers and lengths; Plate III: e,f) were used. Complexity of these forms was understood to increase with both the number and the length of spines. Quantification of the x axis (Fig. 4) was rather problematic in this case, so data were arranged in order of complexity, identified by a serial number for the form.

Forms 1–10 (Fig. 4, × axis) were rather simple corresponding to *T. glabrum* (1) with no spines and *T. hastiferum* (2–10) with 4 spines, one on each of the four cells of the coenobium but of varying length. Forms 3 and 6 (open circles on Fig. 4) were different in having the 4 spines placed on separate cells but close to each other (this way appearing chiefly on one side of the coenobium). This artificial asymmetry (in nature, the spines are arranged at the greatest possible distance from each other) decreased the form resistance well below that of the naked (1) form. Nevertheless, at $\leq$4 spines, their lengths imposed no trend-like changes in the form resistance. Forms 11–25 corresponded to *T. staurogeniaeforme* or *T. hortobagyi* and these species were assigned because natural populations are very rich in the variety of detailed form (see Hindák, 1980, 1984; Komárek & Fott, 1983). Increasing complexity (in terms of both increasing number and length of spines) resulted in a significant (2–3 fold) increase of Φ unless the spines were arranged very asymmetrically (forms 14, 16, 17, 22, 23, 24; open circles on Fig. 4).

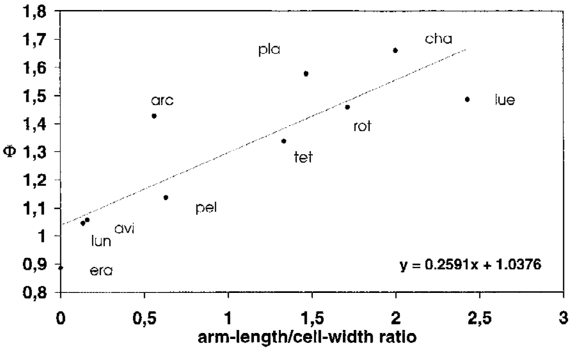

Figure 5. Dependence of the form resistance factor (Φ) on the arm-length/cell-width ratio of different *Staurastrum* forms (modelling material). Abbreviations – arc: *St. arcuatum*; avi: *St. avicula*; cha: *St. chaetoceras*; era: *St. erasum*; lue: *St. luetkemuelleri*; lun: *St. lunatum*; pel: *St. pelagicum*; pl: *St. planktonicum*; rot: *St. rotula* and tet: *St. tetraceras*.

Shapes of 11 *Staurastrum* spp. and 4 *Cosmarium* spp. (Plate II: d–q) were tested for form resistance (modeling material). Each of the *Cosmarium* spp. had $\Phi < 1$ which means that they sink faster than the volume-equivalent sphere (Table 1). *C. ornatum* was manufactured in duplicate: one with smooth surface (artificial form) and the other with papillate surface (natural forrm). This difference in morphology resulted in slightly higher form resistance in the papillate form. For *Staurastrum* spp., a significant correlation ($r = 0.86$; $n = 9$; $P < 0.1\%$) was found between the arm-length/cell-width ratio and Φ (Fig. 5).

While experimenting with desmids, the most striking phenomenon was their behaviour while sinking. Like in other experiments described above we took care of starting position of the cells. Whatever was the starting position, desmids (including the ones with low from resistance) turned to a position where the longest axis was horizontal. The distance required to perform this turn varied among cell shapes, but always within the first 10–50 cm of sinking and, without exception, reaching the bottom in this position.

Flagellates

It was not the aim of these studies to experiment with flagellar phytoplankton organisms because they are motile and this is probably a more effective tool for remaining in suspension than to evolve according to sinking resistance. Experimental data have shown that flagellates with a simple shape (*Rhodomonas, Gymnodinium*; Table 1; Plate II: b,c) had $\Phi < 1$ except *Ceratium* (Plate II: a) which fell into the range of other species with protuberances (*Staurastrum*).

Discussion

Rod-like forms are common in several divisions of phytoplankton. Typical representatives are oscillatorean and nostocalean cyanoprokaryota, *Aulacoseira, Planktonema, Mougeotia*. Evolutionary advantage of filamentous shape lays in the fact that they are good light antennae and therefore can photosynthetize with high capacity at low ambient light (Reynolds, 1997). An additional benefit of this shape is the rather strong increase of Φ with increasing length as was also found by Reynolds (1984) in experiments with killed *Aulacoseira italica* filaments with different cell numbers although Φ values in Reynolds' (1984) experiments were considerably higher (2.3–5.1) then in our studies.

If the relationship between Φ and L/D (Fig. 2A, $y = 0.053x + 1.1355$) remains linear at higher L/D ratios (we could not experiment with really long cylinders because size of our aquarium did not allow), for a filament having a diameter of 3 μm and a length of 300 μm Φ is expected as about 6.5 which is quite a high one as compared to others obtained in this study and agrees with Reynolds' (1984) highest data.

Indeed, there might be cases when high form resistance of long filaments significantly contributes to establishment of abundant populations in the upper section of a stratified water column. The best example is the establishment of an '**M**' assemblage (Reynolds et al. 2002) in the eplilimnia in summers like that dominated by *Planctonema lauterbornii* in the Vouglans reservoir, France (Leitão et al., 2003), occurrence of *Mougeotia* in Lake Garda, Italy (Salmaso, 2003), or, as most striking case, the annually recurrent under-ice development of *Aulacoseira baikalensis* in Lake Baikal, Russia (Kozhov, 1963).

As mentioned earlier, starting position of cylinders affected the sinking velocity of the particle. We consider this observation as consequential on experimental conditions only and rather irrelevant in nature (at least for non-motile plankton, see later). If starting our longest (8 cm) cylinder in vertical position, the sinking trajectory (approx. 80 cm) that the aquarium allows is only 10× longer than the filament itself. Moreover, the medium was static. The sinking trajectory of a 80-μm long filament within a 8-m thick epilimnion is 100 000 times longer than the filament itself and the medium is far of being still (convectional currents, wind-induced turbulences, etc.). Therefore, we assume that it will change its sinking position frequently thus averaging the differences that arise from different 'starting' positions if the term 'starting position' can be used for natural situation at all.

Disk-like organisms or rather isodiametrical cylinders with $L/D < 2$ (representatives: most species of Centrales) had a rather uniform Φ, therefore slight species-specific differences in their Φ probably do not contribute significantly to selection of a particular species in a given lake.

Colony formation of phytoplankton is usually viewed as a major tool for maintenance high physiological activity rates (since it depends on cell size) and at the same time avoiding grazing (since it depends on colony size). Both species tested in these experiments are common and very successful ones, moreover, they are among the few species for which earlier Φ records are published. For *Asterionella*, our results are in perfect agreement with Reynolds' (1984) findings in two respects: (i) Φ values in his experiments ranged from 2.5 to 4.3 for 1–16 celled colonies while our range was 1.6–4.9 for 1–14 celled colonies, and (ii) he also found almost an linear increase of Φ for 1–6 celled colonies and then Φ remained practically constant. Actually, the latter observation was the most convincing in respect that the method used in this study is an appropriate tool for studying sinking properties, despite the fact that the dimensions applied here were considerably magnified. In the case of *Fragilaria crotonensis*, Φ ranges also agreed with other published data (2.9–6 for 1–20 celled chains in Reynolds [1994] and 4.4–8.1 for 1–14 celled chains in our experiment); increase of Φ with cell number of the chain was close to linear, and, unlike *Asterionella*, apparently did not have an upper limit.

It should be mentioned that losing form resistance by fragmentation of the colony is not necessarily disadvantageous for the population. Fast growing populations of *Asterionella* consist typically of colonies with 8 or 16 cells, which have the highest Φ that this species can attain. If population decline starts – for whatever reason (parasites, depletion of nutrients, etc.) – colonies usually split into 1–3 celled fragments that sink in to the hypolimnion where the causes of population decrease do not prevail. There, they can perrenate and give a start for a new development, if and when environmental conditions allow. This recurrent behavior of *Asterionella* populations is well known.

There is quite a number of species or closely related species that have straight and coiled morphotypes. Examples include *Planktolyngbya limnetica* (straight) – *P. contorta* (coiled); straight and spiraling morphotypes of *Cylindrospermopsis raciborskii* (Fabbro et al., 1996; Baker, 1996); *Pseudanabaena limnetica* (straight) – *P. contorta* (coiled; Kling & Watson, 2003); *Gloeotila pelagica* (straight) – *G. spiralis* (coiled; Schmidt, 1994); *Aulacoseira granulata* var. *angustissima* and *Aulacoseira granulata* var. *angustissima* Morphotype *curvata*. The sinking properties of coiled forms have shown that coiling substantially decreases form resistance factors and therefore floating properties of straight or close-to-straight morphotypes are more advantageous. In grazing experiments carried out by Fabbro & Duivevdoorden (1996), *Brachionus rubescens* could ingest straight filaments of *Cylindrospermopsis raciborskii* while grazing on coiled filaments of *C. raciborskii* was not observed. Little is known about ecological advantages or disadvantages of coiling, however, it seems apparent that coiling decreases form resistance but increases resistance to grazing.

Experiments with star-like forms (*Asterionella*) and coenobia with spines (*Tetrastrum* colonies) have shown that symmetry of a cell or of group of cells have a high impact on Φ: symmetric forms have a higher form resistance than asymmetric ones and the relationship seems to be linear or close to linear. However, as found in the case of *Pediastrum*, certain kinds of symmetry features (arrangement of holes) do not affect the hydrodynamic properties of a sinking particle. Indeed, non-motile planktonic species in nature are frequently symmetric in both the arrangement of cells (if they are colonial) and in the external structures (like spines) on their surfaces. This symmetry in itself can be viewed as a tool to maximize resistance to sinking.

Protuberances and spines are rather common in phytoplankton groups Xanthophyceae, Chrysophyceae, Bacillariophyceae, Chlorococcales and Desmidiales. Such structures increase cell dimensions significantly without being too expensive in terms of cell energetic investment. For this reason, they are acknowledged defence mechanisms against zooplankton grazing. This early assumption got a solid support by experimental observations that spine development in some chlorococcalean algae can be triggered by infochemicals released by zooplankton (e.g. Schlütter et al., 1987), thus being a clear antigrazing property. Additionally (in some groups probably exclusively), spines are an effective tool to increase form resistance in case they are in symmetric arrangement on the cell/coenobium surface. Prior to this study, Conway & Trainor (1972) showed that *Scenedesmus* strains with spines sank more slowly than others without spines. Smayda & Boleyn (1966) found that spineless pre-auxospore cells of the marine diatom *Rhizosolenia setigera* sank faster than those with spines. In experiments when spines of *Thalassiosira weissflogii* were removed with chitinase (Walsby & Xypolyta, 1977): treated cells sank twice as fast as untreated ones. These early findings resulted in a Φ of no higher then 2. From our experiments, it can be extrapolated that very spiny cells/coenobia like *Micractinium*, *Chrysosphaerella* and most species of Heliozoa may have a Φ up to 4 and therefore spines may significantly contribute to keeping the cell in suspension.

Planktonic desmids that were studied in this study had rather low form resistance. Even such a complicated form as *Staurastrum rotula* with its alternating 12 arms had a Φ of some 1.5. Nevertheless, we found a significant correlation between arm length relative to cell width and Φ. We suppose that the suspension of planktonic *Staurastrum* species in the summer epilimnia is not due simply to the form resistance of the cells but to their hydrodynamic behavior in a kinetic medium. This deduction is supported indirectly by observations in stratified tropical and temperate lakes: in stratified temperate lakes, desmids often contribute an insignificant portion of total biomass. In tropical lakes, however, they can dominate in the epilimnion. This observation seems to be contradictory to the implication of the Stokes equation: sinking of a particle of given density and form resistance should sink faster in a tropical epilimnion than in a temperate one, simply because of the lower density of the medium. In order to understand their dominance in some tropical lakes, we have to compare the hydrodynamic properties of lakes at different latitudes. Owing to the wide extremes of day-night temperature variations in the tropics, either the whole water column (atelomixis) or at least the epilimnion (partial atelomixis) is subjected to daily overturn (Barbosa & Padisák, 2003). Thus, particles that manage to remain in the epilimnion in the stagnating diurnal phase of the day experience a robust redistribution during the hours of darkness. Night-time convection is generally much weaker in temperate latitudes, so particles with insufficient resistance to sinking fail to remain in the epilimnion during calm periods.

As was hypothetized in earlier works (McNown & Malaika, 1950), teardrop-shaped forms, like *Rhodomonas* and *Gymnodinium*, have a $\Phi < 1$. Reynolds' (1984) contention that small projections or irregularities of the cell shape or on the cell surfaces do not greatly reduce sinking velocity was clearly upheld in this study. For this reason, we do not suppose that other forms common among the Cryptophyta and Dinophyta would have markedly different Φ. There is an exception to this: *Ceratium* which a very successful genus both in freshwater and sea. It is a powerful swimmer; it is generally too big to be grazed; it has a clear diurnal migration pattern to avoid photoinhibition yet still harvest sufficient light energy to support net photosynthetic gain; and it can migrate to nutrient-rich deeper layers to suffice its nutritional demands if the epilimnion is seriously nutrient depleted (Heaney & Talling, 1980). As shown here, Φ in *Ceratium* 2–3 times greater than other flagellates. We suppose that the energetic cost to *Ceratium* of remaining in the required vertical layer is lower than that to other flagellates and this may contribute to success of this genus.

Although no chrysoflagellate was tested in these studies, it is tempting to extrapolate from this study to other algal groups. Forms of individual species in Euglenophyta, Dinophyta, Volvocales and Chrysophyta are quite similar in the context of their probable form resistance. Species of these groups Euglenophyta, Dinophyta, Volvocales are powerful swimmers (Sommer, 1988). Chrysophytes are not successful swimmers. Most unicellular chrysophytes inhabiting the epilimnia of stratified lakes are too small to be efficient swimmers (Sommer, 1988). Colonies comprising many flagellated cells (like *Uroglena*) cannot reach high unidirectional speed because flagellar movement of individual cells in the colony is not synchronized (Sandgren, 1988), as is the case in the superficially similar colonies of *Volvox*. In this way, it seems quite likely that the high morphological variability that is observed among the chrysoflagellates (like spines of *Bitrichia* or *Stephanoporos*, and silica spines in the genera *Mallomonas, Chrysosphaerella, Spiniferomonas*) were evolved to help their otherwise handicapped flotation.

When discussing form resistance of phytoplankton species, it is difficult to avoid mentioning the so called "vital factor". It has been demonstrated by a number of workers (Smayda & Boleyn, 1965; Eppley et al., 1967; Smayda, 1970, 1974; Reynolds, 1973; Titman & Kilham, 1976; Wiseman & Reynolds, 1981) that dead or even living but senescent algae sink faster than viable cells, by factors of three to five, but without any visible

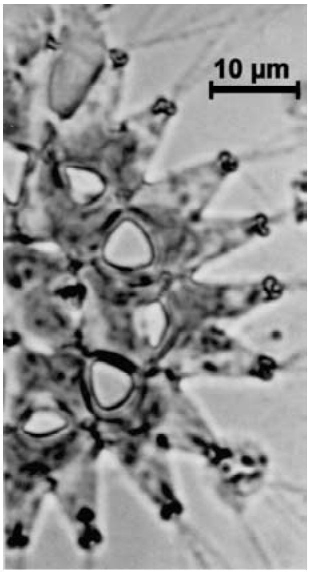

Figure 6. Pediastrum duplex from River Elbe. Note the mucilageus protuberances emerging on the marginal cells. (Photo: L. Krienitz. Published with allowance by L. Krienitz).

alteration in shape, size or form-resistant structures. Since this vital factor remains mysterious, Reynolds (1984) concluded that it is advantageous to separate its contribution to Φ by investigating form resistance in killed cells. This advice was wholly followed in this study, insofar as there is no vital contribution to the sinking behaviour of PVC. However, it is opportune to speculate what this vital factor might be.

Phytoplankton ecologists routinely work with Lugol-preserved samples and recent taxonomists are mostly busy investigating 16S rDNA sequences of cultured algae. One of the consequences is that many, seemingly unimportant, structures remain hidden, although they were quite evident for old-time taxonomists insistent on working with freshly collected living material. These structures include, for example, mucilage stalks or spine-like protuberances often surrounding the cells. On a photo published by Canter-Lund & Lund (1995; Fig. 37) a *Pediastrum* coenobium is seen with hardly visible mucilage stalks initiating on marginal cells. These structures are much more apparent on the photograph (Fig. 6) of a *Pediastrum duplex* from River Elbe: the specimen had numerous such structures originating from the marginal cells and radiating outwards. According to personal communication of the original observer, Dr Lothar Krienitz (see also Krienitz, 1990), these mucilage protuberances had lengths corresponding roughly to the diameter of the coenobium and the photo was taken on a freshly collected coenobium which was dried in under the microscope. Also in a dry preparation documented in Canter-Lund & Lund (1995, Fig. 214) a *Cyclotella* cell is seen with 10–15 times longer non-siliceous protuberances than the diameter of cell. Drying of freshly collected specimens seem to be an effective tool to make visible protuberances of algal cells and staining can be the other one: Canter-Lund & Lund (1995; Fig. 60) published the photograph of a *Staurastrum* stained with brilliant crystal blue and showing fine protuberances most probably made of mucilage stalks.

They might easily disintegrate when the cell is killed or even when they are merely senescent. We never see these structures in preserved materials even if methylene-blue staining or Indian-ink contrasting is applied. Needless to say that presence of such structures may significantly increase Φ and it is also probable that such flexible soft structures do not prevent grazing and therefore did not evolve for predation defense tool.

Another important kind of vital contribution to form resistance might be the ability of the living organism to maintain the position that provides the highest form resistance. As shown above, our *Tetrastrum* forms with many spines on only one side of the coenobium turned to ‘spines up’ position very rapidly and in this position they sank faster than the equivalent forms lacking spines altogether. If species with such asymmetrically arranged protuberances are motile, a main role of its motility can be to maintain a certain orientation of the cell in which ensures maximum form resistance. In phytoplankton, such species might include *Mallomonas tonsurata, M. corymbosa* and *M. cyathellata*. We cannot see position and swimming behavior in living, motile *Mallomonas* but we can see that of jellyfish, one of the biggest members of marine plankton. Medusae have jelly arms varying in numbers and size and they are invariantly below the main body of the living animal. We may even observe how they use their jelly arms for flotation between two active movement events. Note: this position of the arms is just the opposite from that we observed in asymmetric artificial *Tetrastrum* shapes. If a jellyfish is dead, it rolls in the water: the animal is visibly drifting in a rather random position and the jelly arms or their visible rests are never as beautifully arranged and symmetric as when they are living. It may follow that positioning of the cell, even in phytoplankton, is an essential vital component of sinking especially for non-symmetric planktonic plants or animals with at least some motility.

Form resistance is of course not the only adaptive mechanism for enhancing flotation of plankton. Planktonic animals and most flagellate phytoplankton species are quite efficient in vertical positioning. Cyanoprokaryota have very effective mechanisms for regulating the buoyancy provided by their gas vesicles or aerotopes. Mucilage seems to be a flotation-aid however the mechanisms are unclear since on one hand it decreases the density of the organism but, on the other hand, increases its size. However, on basis of the Stokes' equation, we have to see that decrease of density, for example by mucilage secretion, is an ultimate tool for remaining in suspension: an organism with density equaling the density of the medium will float independently of size or shape.

It is difficult to assess how much mere form resistance has contributed to the evolution of planktonic species or to the selection of specific phytoplankton assemblages. Nevertheless, differences in form resistance can be decisive in some cases and it can also be supposed that at least part of the overall morphological diversity of plankton developed under evolutionary driving force of form resistance optimisation.

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