

Reprinted from
28 May 1976, Volume 192, pp. 885-887

SCIENCE

Surface/Volume Ratio: Implications for Phytoplankton Morphology

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Surface/Volume Ratio: Implications for Phytoplankton Morphology

Abstract. *Plankton autotrophs vary greatly in size and shape. Computation of surface/volume ratios for biomass units of 27 coexisting phytoplankton species in a tropical lake indicates that these ratios are conserved within a range much narrower than expected by random choice of shapes. Conservation of surface/volume ratios suggests new explanations for the shapes of phytoplankton biomass units.*

The surface/volume ratio of a biomass unit influences its uptake of light and nutrients, its release of waste products and heat, and its loss of useful compounds or admission of toxins. Natural selection and competition must therefore influence the surface/volume (S/V) ratio of organisms. Such an assumption is the foundation for standard interpretations of Bergman's and Allen's rules for shape of homeotherms (1). Selection for a particular range of S/V ratios must restrict shape for organisms of a particular biomass or restrict biomass for organisms of a particular shape. The following analysis of the S/V ratios of phytoplankton biomass units in nature shows that variation of the S/V ratio is more restricted than expected and that this restriction probably influences phytoplankton shape.

The balance of selective pressures affecting dimensions, volume (mass), and S/V ratio is of particular interest in plankton habitats, where a large number of simple autotrophic species nourish themselves by uptake of nutrients through the surface of small biomass units. The phytoplankton of lakes generally con-

sists of 50 to 100 species of algae ranging in size between 1 and 200 μm and competing on the common basis of autotrophy in a nutrient broth. Culture of phytoplankton shows that virtually all species have plastic morphological potential with respect to both size and shape (2). Specimens taken from a single habitat in nature vary much less than the full potential of the species. Deduction and experimentation suggest that grazing (3) and sinking (4) restrict morphological variation. Another possibility, the direct effect of the S/V ratio on uptake and loss of materials, has received less consideration as a determinant of size and shape (5).

Taxonomists have long recognized intraspecific variation of linear proportions in algae (6), as this phenomenon reduces the taxonomic value of measurements. In general, larger specimens are more attenuate than smaller ones of the same species. More recently, laboratory culture of a common chlorophyte has shown that the linear proportions and S/V ratios of clones change predictably in response to temperature (7). Laboratory

evidence also suggests that the nutrient uptake potential of algae is strongly affected by the S/V ratio (8).

The following analysis is based on the S/V ratios of all autotrophic community members from the plankton of Lake Lanao, Philippines. Lake Lanao is a large natural lake located on the island of Mindanao (8°N, 124°E) (9). Plankton primary production is high, as is often true of tropical lakes (10), but nutrient input is moderate and mostly from natural sources. The phytoplankton includes 70 species of autotrophs, but the present analysis is restricted to the 27 most abundant species, which account for 98 percent of the annual standing crop biomass. The remaining species share insignificantly in the partitioning of community resources. Table 1 gives the taxonomic affinity, mean volume, surface area, and greatest axial linear dimension (GALD) for 25 of the 27 most abundant species. Two of the 27, *Aphanthece nidulans* (Cyanophyta) and *Kirchneriella elongata* (Chlorophyta), are segregated for special consideration because the cells are dispersed in a gelatinous matrix, which raises problems in computation of S/V ratios.

The statistics in Table 1 are based on measurements of naturally occurring biomass units over an 18-month study period (11). The number of cells in an average biomass unit for each species is indicated in Table 1, as is the general shape of each unit. The volume and surface area of biomass units were computed

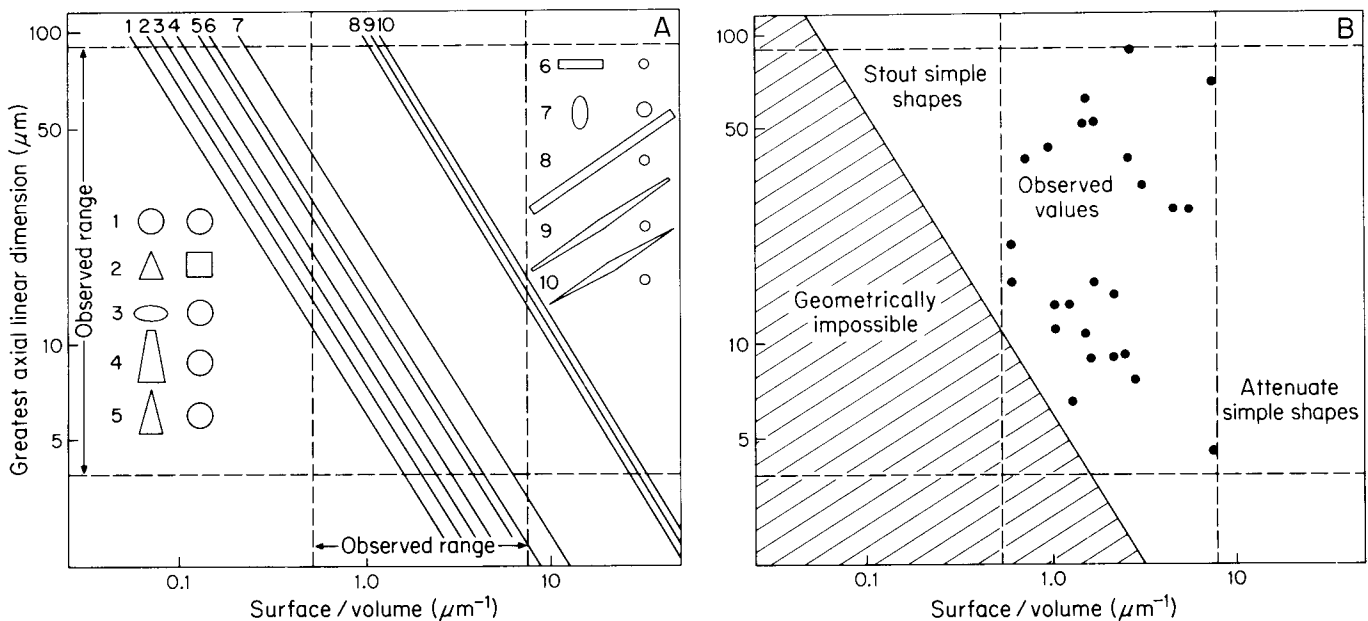


Fig. 1. Relation of the greatest axial linear dimension (GALD) and surface/volume ratio for (A) selected simple geometric solids and (B) the 25 most abundant phytoplankton species of Lake Lanao, Philippines. The geometric shapes in (A) are shown from perspectives perpendicular to the longest and shortest axes. Figures shown are: 1, sphere; 2, pyramid; 3, prolate ellipsoid; 4, stout cone frustrum; 5, stout cone; 6, stout cylinder; 7, oblate ellipsoid; 8, slim cylinder; 9, slim double cone frustrum; and 10, slim double cone. The ratio of the linear dimensions for the solids is shown to scale.

from their shapes and dimensions. In many cases, the computations involved the use of composite shapes or of other special considerations not indicated in Table 1, such as exclusion of abutments between cells from the surface area of the biomass unit.

Figure 1A shows the relation between S/V ratio and GALD for a variety of simple geometric shapes common among lacustrine phytoplankton. Superimposed are the ranges of observed S/V and GALD values for the Lanao phytoplankton species. A minimum value of S/V for any particular value of GALD is given by the line representing a sphere. Values of S/V below this line are geometrically impossible (Fig. 1B).

A wide variety of simple geometric shapes have S/V values below the range of values observed in Lake Lanao, even when GALD is within the observed range (Fig. 1A). Similarly, a number of attenuate simple shapes have S/V values above the observed maximum value when GALD is within the observed range for the Lake Lanao species. Thus Fig. 1 shows that if the shapes corresponding to particular values of GALD

were chosen at random, the range of S/V values would be much larger than it is in Lake Lanao. The S/V ratio is apparently conserved by selection of appropriate shapes according to the volume of the unit, or by selection of appropriate volume according to the shape of the unit.

The conservation of S/V ratio may contribute to some new explanations of phytoplankton morphology. Phytoplankton biomass units, which ordinarily consist of 1 to 50 cells, show four levels of structure: (i) primary structure, determined by the shape and size of cells comprising the biomass unit; (ii) secondary structure, determined by the arrangement of cells with respect to each other as a result of physical connections between them; (iii) tertiary structure, resulting from coiling, twisting, or bending of multicellular units; and (iv) quaternary structure, arising from the combination of similar multicellular subunits. Less than half of phytoplankton species show only primary structure, half or more show secondary structure, and only a few show structure at all levels.

If selection limits the volume or GALD of any particular species, then

the principle of S/V conservation, as documented empirically in Fig. 1, will limit the potential shape of the biomass unit. Units of high volume cannot assume simple nonattenuate geometric shapes without falling below an acceptable competitive S/V limit (Fig. 1B). There are two possible strategies for such high-volume units: (i) adoption of attenuate shape and (ii) dissection of biomass into multiple but contiguous units of smaller volume—that is, adoption of secondary structure. The first alternative necessitates an increase in GALD, which undoubtedly has certain disadvantages, but the second alternative minimizes this requirement. The two strategies occur singly and in combination in nature. The principle of S/V conservation may thus explain the frequency in natural phytoplankton assemblages of the attenuation of large biomass units and of secondary structure, which is a common but mysterious aspect of phytoplankton morphology.

For species having very small volumes, the observed conservation of S/V ratio suggests that an undesirably high S/V ratio would be produced by many otherwise possible shapes. The adaptive options in this case are different from those for species with high volumes. The simplest adaptation is a stout shape, which reduces the S/V ratio for a particular volume. Stout shapes in fact predominate among very small species. An alternative or supplementary strategy is a decrease in the surface area of the unit without an increase in its biomass. This can be accomplished by dispersion of the cells in a physiologically inactive matrix. In Lake Lanao the species of *Kirchneriella* and *Aphanothece* mentioned above show this morphology. The individual cells of either species, if free in the water column or joined in tandem, would have an S/V ratio above the observed limit for Lake Lanao. The matrix, because of its imperfect porosity, evidently lowers the effective S/V ratio to an acceptable competitive value. The bulky matrix may have other advantages as well, but its prominence in two species having otherwise extreme S/V ratios is strong circumstantial evidence that the S/V ratio is a determining factor for this morphotype.

In the foregoing discussion rare species have been excluded on the grounds that they do not compete successfully for a significant share of community resources. If rare species were included, the observed upper limits of S/V ratio and GALD would remain unaltered. The lower limit of GALD would also remain unaltered, although some small *Chlorella*

Table 1. List of the 25 taxa discussed in the text and the volume, surface area, and greatest axial linear dimension (GALD) for average biomass units of each.

Taxon	Cells per unit	Volume (μm^3)	Area (μm^2)	GALD (μm)	General shape
Cyanophyta					
<i>Chroococcus minutus</i>	4	280	530	13	Sphere
<i>Dactylococcopsis fascicularis</i>	1	10	50	26	Double cone
<i>Dactylococcopsis woltrecki</i>	1	15	60	25	Double cone
<i>Anabaena sphaerica</i>	12	246	554	38	Joined spheres
<i>Anabaena spiroides</i>	30	1000	1413	48	Joined spheres
<i>Lyngbya limnetica</i>	15	24	174	61	Cylinders
Chlorophyta					
<i>Tetraedron minimum</i>	1	25	62	7	Frustrum composite
<i>Sphaerocystis Schroeteri</i>	6	480	706	15	Sphere
<i>Oocystis submarina</i>	2	140	201	8	Prolate ellipsoid
<i>Oocystis lacustris</i>	2	500	452	12	Prolate ellipsoid
<i>Chodatella subsalsa</i>	2	250	226	10	Prolate ellipsoid
<i>Chodatella</i> sp.	1	40	80	8	Prolate ellipsoid
<i>Ankistrodesmus setigerus</i>	1	35	95	30	Double cone
<i>Dictyosphaerium pulchellum</i>	10	500	660	50	Multiple spheres
<i>Dimorphococcus lunatus</i>	10	700	940	55	Multiple prolate ellipsoids
<i>Coelastrum cambricum</i>	35	2500	2186	40	Joined spheres
<i>Scenedesmus ecornis</i>	4	480	540	12	Rounded cylinders
<i>Scenedesmus</i> sp.	4	100	185	8	Rounded cylinders
<i>Coccomyxa</i> sp.	1	2	14	4	Rounded cylinder
Chrysophyceae					
<i>Chromulina</i> sp.	1	100	113	6	Sphere
Bacillariophyceae					
<i>Nitzschia baccata</i>	1	190	440	80	Double frustrum
<i>Melosira granulata</i>	4	1200	735	36	Cylinder
Dinophyceae					
<i>Gymnodinium</i> sp.	1	1200	615	14	Sphere
Cryptophyceae					
<i>Rhodomonas minuta</i>	1	70	95	10	Flattened frustrum
<i>Cryptomonas marssonii</i>	1	1200	650	19	Flattened frustrum

(of about 4 μm in size) would approach the limit shown in Fig. 1. These *Chlorella* seem to belong to more than one species, no one of which is sufficiently numerous to be included in the top 25 species. The observed lower limit of S/V ratio would be exceeded by a single rare diatom, *Melosira agassizi*, which colonizes the open water from the littoral zone during the annual mixing period when turbulence is greatest, but which never becomes very abundant. The inclusion of rare phytoplankton species would therefore result in essentially the same pattern as that shown in Fig. 1. For the purpose of comparing different plankton environments, however, generalizations should not be made on the basis of data from organisms that are not truly planktonic or that are not really capable of exploiting the resources of the plankton environment in question.

The conservation of S/V ratio raises a number of questions that are not fully solvable from the data at hand. The most obvious of these involve mucilage sheaths, the blue-green algae, and the bacterioplankton.

A large number of species, notably the desmids and filamentous blue-greens, are facultatively capable of secreting large mucilage sheaths around the biomass units. Mucilage sheaths are thought to retard sinking (4) and to inhibit digestion by herbivores in some cases (12). It is also possible that sheaths beneficially lower the effective S/V ratio, or that their merits in the retardation of sinking and digestion are balanced against a detrimental increase in effective S/V ratio at any particular time of year. Flexibility in secretion of a sheath would obviously have selective value if the optimal S/V ratio changes over the year.

The blue-greens constitute a special subgroup of the phytoplankton in that they are prokaryotic and often have dis-

tinctive features, including capacity for buoyancy regulation and nitrogen fixation (4) and probably low food value for zooplankton (13). Some of these species are thus partially exempt from the problems of sinking, grazing, and nitrogen depletion that are shared by most taxa. The blue-greens of Lake Lanao fall within the GALD and S/V ranges observed for other taxa. However, the Lanao blue-greens do have a higher average S/V ratio than the other Lanao taxa ($P < .01$, Wilcoxon two-sample test). The selective forces that act to increase the volume and S/V ratio of biomass units may not operate so effectively in the blue-greens because of their special characteristics.

The bacterioplankton are not included in the foregoing discussion as they are, for the most part, not autotrophic. If the metabolically active bacteria were added to Fig. 1, the lower limit of GALD would have to be moved down to 1 μm or less, but the observed range of S/V ratios would probably not be expanded. Although bacteria in the water column have high average S/V ratios, they are spherical or stoutly cylindrical in shape and can thus be equaled or exceeded in S/V ratio by several autotroph species. For example, it is clear from Fig. 1 that a unicellular coccoid form with a diameter of 1 μm would have a lower S/V ratio than several of the phytoplankton species. The bacterioplankton therefore appear to fit with the scheme of S/V conservation observed in the phytoplankton. Whether this is due to the operation of common selective pressures or is merely fortuitous is unclear.

The exact dispersion of phytoplankton S/V ratios will probably vary from one community to another, but conservation of the S/V ratio is likely to be widely observed in nature, as the balance of selective pressures affecting the ratio is common to the phytoplankton in general. If

further studies verify the conservation of S/V ratio, a new set of explanations is available for phytoplankton morphology.

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References and Notes

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11. A few phytoplankton species, mostly chlorophytes, bear long spines. Examples are *Chodatella* and some *Scenedesmus*. Such physiologically inactive parts alter shape but not S/V ratio. In Lake Lanao, only two of the top 27 species bear spines. My computations are based on the main biomass unit exclusive of spines, but conclusions are similar if spines are included.
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14. Supported by NSF grants GB41293 and BMS 75-03102. I thank R. Pennak and J. Bushnell and unnamed reviewers for reading the manuscript.

8 December 1975; revised 23 February 1976