Surface/Volume Ratio: Implications for Phytoplankton Morphology

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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 consists 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, Aphanathece nidulans (Cyanophyta) and Krichneriella elongata (Chlorophyta), are segregated for special consideration because the cells are dispersed in a gelatious 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 frustum; 5, stout cone; 6, stout cylinder; 7, oblate ellipsoid; 8, slim cylinder; 9, slim double cone frustum; and 10, slim double cone. The ratio of the linear dimensions for the solids is shown to scale.](image-url)
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 phytoplank-
ton 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 im-
possible (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 corre-
responding 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 vol-
ume according to the shape of the unit.

The conservation of S/V ratio may con-
tribute to some new explanations of phytoplankton morphology. Phytoplank-
ton biomass units, which ordinarily consist of 1 to 50 cells, show four levels of
structure: (i) primary structure, deter-
mined by the shape and size of cells com-
prising the biomass unit; (ii) secondary
structure, determined by the arrange-
ment of cells with respect to each other
as a result of physical connections be-
tween them; (iii) tertiary structure, re-
sulting 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 as-
sume simple nonattenuate geometric
shapes without falling below an accept-
able 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 bio-
mass 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 disad-
advantages, but the second alternative
minimizes this requirement. The two
strategies occur singly and in combina-
tion in nature. The principle of S/V
conservation may thus explain the fre-
cuency in natural phytoplankton assem-
bilages of the attenuation of large bio-
mass units and of secondary structure,
which is a common but mysterious as-
pert of phytoplankton morphology.

For species having very small vol-
umes, the observed conservation of S/V
ratio suggests that an undesirably high
S/V ratio would be produced by many oth-
erwise possible shapes. The adaptive op-
tions in this case are different from those
for species with high volumes. The sim-
plest adaptation is a stout shape, which
reduces the S/V ratio for a particular vol-
ume. 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 ac-
complished 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 imper-
fect porosity, evidently lowers the effec-
tive S/V ratio to an acceptable com-
petitive value. The bulky matrix may
have other advantages as well, but its
prominence in two species having other-
wise extreme S/V ratios is strong circum-
stantial evidence that the S/V ratio is a
determining factor for this morphotype.

In the foregoing discussion rare spe-
cies have been excluded on the grounds
that they do not compete successfully for
a significant share of community res-
ourses. 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*

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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.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Cells per unit</th>
<th>Volume (µm³)</th>
<th>Area (µm²)</th>
<th>GALD (µm)</th>
<th>General shape</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyanophyta</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chroococcus minutus</em></td>
<td>4</td>
<td>280</td>
<td>530</td>
<td>13</td>
<td>Sphere</td>
</tr>
<tr>
<td><em>Dactylococcus fasciculatus</em></td>
<td>1</td>
<td>10</td>
<td>50</td>
<td>26</td>
<td>Double cone</td>
</tr>
<tr>
<td><em>Dactylococcus woltereki</em></td>
<td>1</td>
<td>15</td>
<td>60</td>
<td>25</td>
<td>Double cone</td>
</tr>
<tr>
<td><em>Anaebana sphaerica</em></td>
<td>12</td>
<td>246</td>
<td>554</td>
<td>38</td>
<td>Joined spheres</td>
</tr>
<tr>
<td><em>Anaebana spiroides</em></td>
<td>30</td>
<td>1000</td>
<td>1413</td>
<td>48</td>
<td>Joined spheres</td>
</tr>
<tr>
<td><em>Lyngbya limnetica</em></td>
<td>15</td>
<td>24</td>
<td>174</td>
<td>61</td>
<td>Cylinders</td>
</tr>
<tr>
<td>Chlorophyta</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tetraedron minimum</em></td>
<td>1</td>
<td>25</td>
<td>62</td>
<td>7</td>
<td>Frustrum composite</td>
</tr>
<tr>
<td><em>Sphaerocystis schroeteri</em></td>
<td>6</td>
<td>480</td>
<td>706</td>
<td>15</td>
<td>Sphere</td>
</tr>
<tr>
<td><em>Oocystis submarina</em></td>
<td>2</td>
<td>140</td>
<td>201</td>
<td>8</td>
<td>Prolate ellipsoid</td>
</tr>
<tr>
<td><em>Oocystis lacustris</em></td>
<td>2</td>
<td>500</td>
<td>452</td>
<td>12</td>
<td>Prolate ellipsoid</td>
</tr>
<tr>
<td><em>Chodatella subalsa</em></td>
<td>2</td>
<td>250</td>
<td>226</td>
<td>10</td>
<td>Prolate ellipsoid</td>
</tr>
<tr>
<td><em>Chodatella sp.</em></td>
<td>1</td>
<td>40</td>
<td>80</td>
<td>8</td>
<td>Prolate ellipsoid</td>
</tr>
<tr>
<td><em>Ankistrodesmus setigerus</em></td>
<td>1</td>
<td>35</td>
<td>95</td>
<td>30</td>
<td>Double cone</td>
</tr>
<tr>
<td><em>Dictyosphaerium pulchellum</em></td>
<td>10</td>
<td>500</td>
<td>660</td>
<td>50</td>
<td>Multiple spheres</td>
</tr>
<tr>
<td><em>Dimorphochloris lunatus</em></td>
<td>10</td>
<td>700</td>
<td>940</td>
<td>55</td>
<td>Multiple prolate</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>ellipsoids</td>
</tr>
<tr>
<td><em>Coelastrum cambricum</em></td>
<td>35</td>
<td>2500</td>
<td>2186</td>
<td>40</td>
<td>Joined spheres</td>
</tr>
<tr>
<td><em>Scenedesmus ecornis</em></td>
<td>4</td>
<td>480</td>
<td>540</td>
<td>12</td>
<td>Rounded cylinders</td>
</tr>
<tr>
<td><em>Scenedesmus sp.</em></td>
<td>4</td>
<td>100</td>
<td>185</td>
<td>8</td>
<td>Rounded cylinders</td>
</tr>
<tr>
<td><em>Coccomyxa sp.</em></td>
<td>1</td>
<td>2</td>
<td>14</td>
<td>4</td>
<td>Rounded cylinder</td>
</tr>
<tr>
<td>Chrysophyceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chromulina sp.</em></td>
<td>1</td>
<td>100</td>
<td>113</td>
<td>6</td>
<td>Sphere</td>
</tr>
<tr>
<td>Bacillariophyceae</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nitzschia bacca</em></td>
<td>1</td>
<td>190</td>
<td>440</td>
<td>80</td>
<td>Double frustrum</td>
</tr>
<tr>
<td><em>Melosira granulata</em></td>
<td>4</td>
<td>1200</td>
<td>735</td>
<td>36</td>
<td>Cylinder</td>
</tr>
<tr>
<td>Dinophyceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gymnodinium sp.</em></td>
<td>1</td>
<td>1200</td>
<td>615</td>
<td>14</td>
<td>Sphere</td>
</tr>
<tr>
<td>Cryptophyceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Rhodomonas minuta</em></td>
<td>1</td>
<td>70</td>
<td>95</td>
<td>10</td>
<td>Flattened frustum</td>
</tr>
<tr>
<td><em>Cryptomonas marssonii</em></td>
<td>1</td>
<td>1200</td>
<td>650</td>
<td>19</td>
<td>Flattened frustum</td>
</tr>
</tbody>
</table>
(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 distinctive 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 autotrophic species. For example, it is clear from Fig. 1 that a unicellular coccolid 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.

**References and Notes**

1. Some of the standard interpretations of these rules are challenged by P. Scholander (Evolution 9: 15 (1955)).


5. W. H. Munk and G. A. Riley (J. Mar. Res. 11, 215 (1952)) have taken a theoretical approach to the interaction between sinking rate, shape, density, and nutrient uptake which is relevant to the control of S/V ratio. Sinking rate, which is dependent on size and shape, can affect the rate of nutrient uptake by controlling the exposure of the cell surface to nutrients. However, a high sinking rate has the disadvantage of removing cells from the lighted zone unless turbulence is great.


11. A few phytoplankton species, mostly chlorophytes, bear long spines. Examples are *Chlorella* 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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