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AN EMPIRICALLY BASED MODEL OF VARIATION IN ROTATIONAL ELEMENTS IN CENTRIC DIATOMS WITH COMMENTS ON RATIOS IN PHYCOLOGY¹

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ABSTRACT

Ratios are commonly used to relate taxonomic, physiological and ecological properties of algal cells to variation in cell shape and size. However, ratios can be more difficult to interpret than the original variables. A detailed example of a ratio commonly used in diatom taxonomy is presented. The abundance of a repeated rotational element on a centric diatom valve is often expressed as density (e.g. number of marginal spines per μm of circumference), rather than simply as total number. It is empirically demonstrated that density is often curvilinearly related to diameter, whereas total number is linearly related (when related at all) to diameter. This linear relationship is the basis for an empirical model which accounts for variation in density in real examples. Under this model, density will be a poorer taxonomic character than total number except under rare occasions (e.g. when the slope of the total element versus diameter regression is zero and variance in the numerator is not dependent on the denominator). Other ratios are similarly difficult to interpret. Length/width (or width/length) is often curvilinearly related to width (length) because variation is compounded from several

sources. Surface/volume has been employed to investigate the relative contributions of size and shape to phytoplankton sinking. However, the properties of this ratio have not been fully investigated, and the relationship between size, shape and sinking rate has not been fully elucidated for the data set in question.

Key index words: blue-green algae; centric diatoms; morphometrics; phytoplankton; ratios; shape; sinking; size

Many fields of algal research utilize ratios of measurements and/or counts of morphological elements to summarize algal morphology. The stated or implicit goal of using ratios such as width/length or surface area/volume is to standardize the numerator for presumed dependence on the denominator, usually trying to adjust for the effect of size. There are many reasons why such attempts can fail. For example, numerator variance may be dependent on the absolute value of the denominator, or a plot of the numerator against the denominator has a non-zero intercept. In such cases, the ratio will still be correlated with its components. Algal examples are discussed in this paper. In short, it seems that a ratio can be more difficult to interpret than the original variables. This issue seems to have been all but ignored by phycologists employing ratios.

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TABLE 1. Regression parameters (s, slope; i, intercept) for total numbers of costae (COS), spines (SPI), labiate processes (LP) and marginal strutted processes (MSP) against diameter. (—) signifies no available data. Data sources: (1) Burke and Woodward (1968–1969); (2) Burke (1970–1972); (3) Genkal (1984); (4) Hickel and Håkansson (1987); (5) Theriot (unpubl.); (6) Haworth (1984); (7) Geissler (1986); (8) Hasle and Fryxell (1977); (9) Genkal and Makarova (1984); (10) Fryxell et al. (1986); and, (11) Theriot and Bradbury (unpubl.). The slope and intercept of the unique setae of *Corethron criophilum* against diameter are 0.23 and 11.3 (5).

Species	COS-s	COS-i	SPI-s	SPI-i	LP-s	LP-i	MSP-s	MSP-i
<i>Actinocyclus actinochilus</i> (Ehrenb.) Simonsen (5)	—	—	—	—	0.23	2.05	—	—
<i>A. curvatus</i> Janisch (5)	—	—	—	—	0.26	2.31	—	—
<i>Aulacodiscus compactus</i> Rattray (1)	—	—	—	—	0.04	2.80	—	—
<i>A. oregonus</i> Harv. and Bail. (1)	—	—	—	—	0.07	0.09	—	—
<i>A. pulcher</i> Norman (2)	—	—	—	—	0.04	3.00	—	—
<i>Azpeitia tabularis</i> (Grunow) Fryxell and Sims (5)	—	—	—	—	0.26	2.31	—	—
<i>Cyclostephanos dubius</i> (Fricke) Round (3)								
(= <i>S. dubius</i>)	2.50	13.30	—	—	—	—	1.41	-2.69
<i>C. dubius</i> (4)	3.10	12.00	—	—	—	—	—	—
<i>C. fenestratus</i> Theriot and Kociolek (5)	1.40	8.10	—	—	—	—	—	—
<i>C. guatemalae</i> Theriot and Bradbury nom. prov. (11)	1.00	10.00	1.00	10.0	—	—	—	—
<i>C. invisitatus</i> (Hohn and Hellerman) Theriot et al. (3)								
(= <i>S. invisitatus</i>)	2.14	23.00	21.40	23.00	—	—	0.90	0.70
<i>C. lacrimis</i> Theriot and Bradbury nom. prov. (11)	0.60	8.90	0.60	8.90	—	—	0.60	8.90
<i>Cyclotella stelligera</i> Cleve and Grunow morphotype designated "other" in (6)	7.73	-7.30	—	—	—	—	1.60	-1.00
<i>C. stelligera</i> (6)	3.20	3.60	—	—	—	—	1.50	-3.00
<i>Stephanodiscus alpinus</i> Hustedt (5)	1.70	14.20	—	—	—	—	1.40	-7.20
<i>S. astraea</i> (Ehrenb.) Grunow (3)	1.30	20.60	—	—	—	—	—	—
<i>S. astraea</i> var. <i>intermedius</i> Fricke (3)	1.81	-2.15	—	—	—	—	—	—
<i>S. binderanus</i> (Kützing) Krieger (3)	0.67	28.00	0.67	28.0	—	—	—	—
<i>S. hantzschii</i> Grunow (7)	2.00	7.80	—	—	—	—	—	—
<i>S. hantzschii</i> (3)	1.85	8.20	1.85	8.20	—	—	—	—
<i>S. makarovae</i> Genkal (3)	2.60	9.00	2.60	9.00	—	—	0.30	3.50
<i>S. minutulus</i> (Kützing) Cleve and Möller (3)								
(= <i>S. astraea</i> var. <i>minutula</i>)	1.90	17.80	—	—	—	—	1.25	-3.75
<i>S. niagarae</i> Ehrenb. (5)	2.20	-17.50	0.70	2.40	0.90	0.20	0.70	2.40
<i>S. perforatus</i> Genkal and Kuzmin (3)	2.25	7.50	2.25	7.50	—	—	0.50	2.00
<i>S. rotula</i> (Kützing) Hendeby (5)	2.10	-7.10	1.20	-6.20	0.10	0.90	1.20	-6.20
<i>S. tenuis</i> var. <i>tener</i> Genkal and Kuzmin (3)	1.00	4.00	1.00	4.00	—	—	—	—
<i>S. tenuis</i> Hustedt (3)	2.00	5.00	2.00	5.00	—	—	0.28	6.72
<i>S. triporus</i> Genkal and Kuzmin (3)	3.08	10.80	3.08	10.80	—	—	1.50	-1.50
<i>S. yellowstonensis</i> Theriot and Stoermer (5)	1.60	-9.90	0.30	3.70	0.20	2.20	0.30	3.70
<i>Thalassiosira conferta</i> Hasle and Fryxell (8)	—	—	—	—	—	—	0.50	1.50
<i>T. guillardii</i> Hasle (9)	—	—	—	—	—	—	3.00	0.00
<i>T. pseudonana</i> Hasle and Heimdal (9)	—	—	—	—	—	—	1.80	3.00
<i>T. tumida</i> (Janisch) Hasle (10)	—	—	—	—	0.08	0.40	—	—
<i>T. weissflogii</i> (Grunow) Fryxell and Hasle (9)	—	—	—	—	—	—	5.40	-30.00

This paper critically examines the behavior of a set of ratios commonly used in centric diatom taxonomy. Fascicles, striae, costae, spines, labiate processes, strutted processes and other elements are often repeated around the diatom valve, exhibiting a degree of rotational symmetry. Morphologic studies of centric diatoms rely increasingly on biometric methods, but there is divergence of opinion of how to express the abundance of rotational elements. The classical measure is density (the ratio of number of an element to some distance along a tangent or the circumference). Measurement along a tangent is recommended in standard diatom references (Anonymous 1975). However, error in tangential density is dependent on specimen size, and circumferential density should be measured if density is to be used at all (Genkal 1977).

It remains unclear why element density has been used as a character almost to the complete exclusion of the total number per valve, particularly since element density is known to have poor statistical be-

havior. For example, fascicle density is dependent on diameter in *Cyclostephanos invisitatus* (Hohn and Hellerman) Theriot et al. (1987) (reported as stria density for *S. invisitatus* in Lowe and Crang 1972), *Cyclostephanos dubius* Round (Hickel and Håkansson 1987) and many species of *Stephanodiscus* Ehrenb., usually in a curvilinear fashion (Genkal 1984). This paper argues that dependency of total number of an element on diameter can be described by a straight line and that variation in regression parameters (slope and intercept) of that relationship have important consequences for correlation between element density and diameter. The statistical anomalies are potentially common to all ratios used to describe algal morphology for physiological, ecological and taxonomic studies.

MATERIALS AND METHODS

Statistics in Table 1 were derived from a variety of sources. Some authors have published raw data (e.g. Burke 1970–1972). Measurements were made by me from diatoms illustrated by oth-

er authors (e.g. *Thalassiosira conferta* Hasle and Fryxell 1977). My own published and unpublished data were included. Material of two species of *Actinocyclus* Ehrenb., *Azpeitia tabularis* (Grunow) G. Fryxell and P. A. Sims, and *Corethron criophilum* Castracane were collected near the island of South Georgia (Theriot and Fryxell 1985). Material of species of *Stephanodiscus* was reported in Theriot and Stoermer (1984a, b, c) and Theriot et al. (1988). *Cyclostephanos* species were from two different fossil deposits in Guatemala and western North America (Theriot and Bradbury, unpubl.). Regression parameters were calculated from raw data where available or from regression lines fit by eye where raw data were expressed as plots in published literature (e.g. Genkal 1984).

Using empirically established limits of intercept and slope (Table 1), a set of experiments was run using PROC GLM in PC-SAS (Statistical Analysis System for Personal Computers, Version 6 Edition; SAS Institute Inc. 1985). The model used was $N = sD + i$ where N equals the total number of a repeated rotational element on a valve; D , valve diameter; s , slope value; and i , the intercept value. Total number of an element was calculated at diameter intervals of $3 \mu\text{m}$ over a range of 3 to $90 \mu\text{m}$, accounting for all but the very smallest and largest centric diatoms commonly encountered. Density was then calculated at $3 \mu\text{m}$ intervals by dividing total number of elements of valve circumference. Slope was held constant and intercept allowed to vary in one set of experiments and vice versa in the second.

RESULTS AND DISCUSSION

Establishment of empirical rule. Published data on covariation of repeated rotationally symmetric elements and diameter are heavily biased towards the family Thalassiosiraceae, mainly *Stephanodiscus*, but several species of *Aulacodiscus* Ehrenb. (Heliopeltaeae) are represented as well (Table 1). Three Hemidiscaceae species and the unusual centric *Corethron criophilum* (Melosiraceae? see Simonsen 1979) were measured for this study to get a rough idea of the generality of the relationships among centric diatoms. Characters included in the survey were spines, strutted processes, labiate processes, costae and the large, serrated setae of *Corethron*. In all cases where a statistically significant relationship exists (i.e. passes some probability test) or is visually apparent, total number of elements can be explained as a linear function of diameter within a species. Plots of data from *Corethron criophilum* and *Azpeitia tabularis*, two non-thalassiosiracean species, illustrate that the linear dependence between number and diameter crosses taxonomic and character boundaries (Figs. 1, 2).

Genkal (1979, 1984) used an exponential equation to describe the pooled among-species relationship between number of rotationally symmetric elements (viz. number of costae and marginal strutted processes, MSP) and diameter. Visual inspection of his *Stephanodiscus* data suggests that linear equations are sufficient to explain costa number–diameter relationship within species (Genkal 1984). In the case of MSP, the exponent (e) of the pooled MSP number–diameter equation (MSP number = diameter ^{e}) is 0.868 suggesting a near linear relationship even for data pooled among species over a wide range of diameters.

When an element number–diameter relationship

appears to exist or has been statistically substantiated, it is always positive. In contrast, apparent element density–diameter relationships are often curvilinear and may be either negative or positive. The relative consistency of element number–diameter covariation (positive and linear) may or may not signify some fundamental rule of diatom development, but it does allow the convenience of speaking of parameters of the element number–diameter regression line as causal variables and parameters of the density–diameter relationship as results. Obviously, this analysis does not identify the underlying causes of variation although it may suggest some.

A model of variation in element density–diameter relationships. Genkal (1977) quantitatively demonstrated that degree of measurement error for tangential density is a function of specimen size. He advocated calculating density as total element number divided by valve circumference (circumferential density). Collins and Groetsch (1981) independently offered a table of values of tangential density for small centrals based on counts of element number over half a valve, but this table was limited to diatoms under $15 \mu\text{m}$ of diameter. I used Genkal's method because there is undoubtedly some error in determining half a valve and because Genkal's method is equally applicable to specimens of all sizes.

The connection between these measurements can be expressed in graphical form (Figs. 3, 4). When slope of an element number–diameter line is varied, the altitude but not the shape of element density line changes correspondingly (Fig. 3). In contrast, the shape of the density–diameter curve is clearly a function of the intercept of the number–diameter line (Fig. 4). Only when the intercept of the number–diameter curve is 0 can there be no relationship between density and diameter. Note that a curvilinear relationship is apparent at small diameters (ca. $5 \mu\text{m}$) even at an intercept of 1. All total number–diameter regressions have average intercept values greater than 1, and costa and spine count intercepts average about 8. A total number–diameter intercept of ± 8 will produce a strongly curvilinear relationship between density and diameter for diatoms between about 0 and $20 \mu\text{m}$ (Fig. 4). Maximum absolute intercept values observed were well over 20 for costa, spine, and marginal strutted process count versus diameter (Table 1). An intercept of only 20 produces a strongly curvilinear relationship between element density and diameter for diatoms between 0 and about $40 \mu\text{m}$ (Fig. 4). Finally, positive intercepts produce negative relationships between density and diameter; negative intercepts produce positive density–diameter relationships (Fig. 4). In summary, the results of this model are consistent in quality with all of the reported covariation (or lack thereof) in density–diameter relationships whether positive or negative, linear or curvilinear.

Examples of the use of number and density in centric diatom taxonomy. Genkal (1984) plotted total element

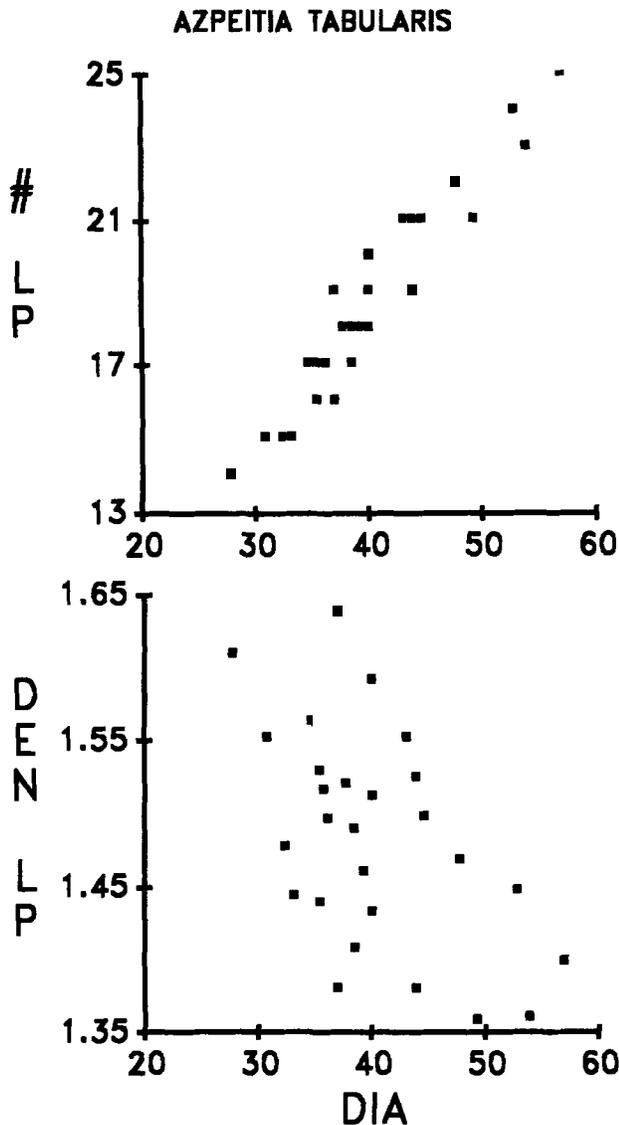


FIG. 1. Number of labiate processes per valve (# LP) and per 10 μm of circumference (DEN LP) versus diameter in μm (DIA) for *Azpeitia tabularis*.

versus diameter and element density versus diameter for a dozen *Stephanodiscus* taxa (see Table 1 for regression statistics). There were no visually apparent deviations from the results predicted by the model. Two species serve as contrasting examples. The intercept of costae number plotted against diameter is about 20 for "*S. astraea* (Ehrenb.) Grunow" (see Håkansson and Locker 1981 for discussion of nomenclature). This high intercept value would predict a negative density-diameter relationship for even a large diatom like *S. astraea* (diameter range was about 18–42 μm). In fact, reported costa density of the smallest specimens was about double that of the largest (8 in 10 μm and 4 in 10 μm , respectively; Figure 2 in Genkal 1984). Density variation should be more pronounced in smaller cells. In fact, costa density of the smallest cell (ca. 4 μm diameter and 27 costae in 10 μm) was nearly triple

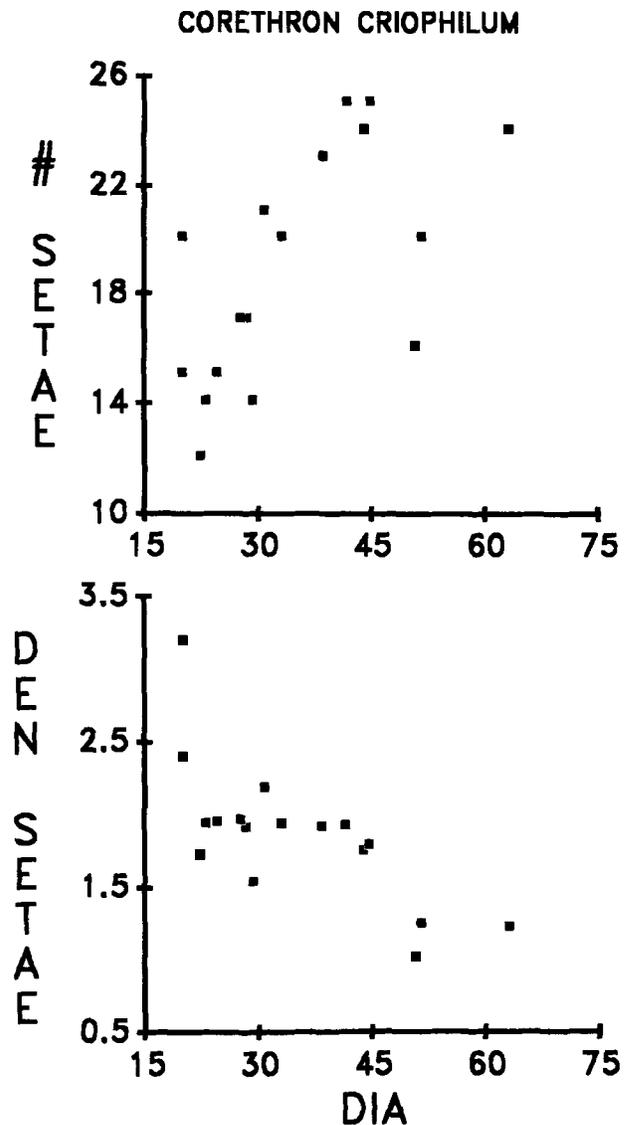


FIG. 2. Number of large serrated setae per valve (# SETAE) and per 10 μm of circumference (DEN SETAE) versus diameter in μm (DIA) for *Corethron criophilum*.

that of the largest (ca. 11 μm diameter and 10 costae in 10 μm) for *S. triporus* Genkal and Kuzmin (Fig. 4 in Genkal 1984).

Hasle and Fryxell (1977) illustrated an abundance of specimens of *Thalassiosira conferta* Hasle and Fryxell (e.g. 12 specimens from their Figs. 7, 8, 12, 15–23), presenting a good opportunity to explore the general usefulness of the empirical model in a genus other than *Stephanodiscus*. Their observation that the number of marginal strutted processes (3–14 MSP per valve) was associated with valve diameter can be confirmed by statistical analysis of their illustrated specimens ($r = 0.95$, $P < 0.0001$; slope = 0.53, $P < 0.0001$; intercept = 1.52, $P < 0.03$). Transforming number to density yields 1.8–2.8 MSP per 10 μm of circumference. Calculated densities can be inverted to yield distances of 3.5–5.7 μm between strutted processes, in good agreement with

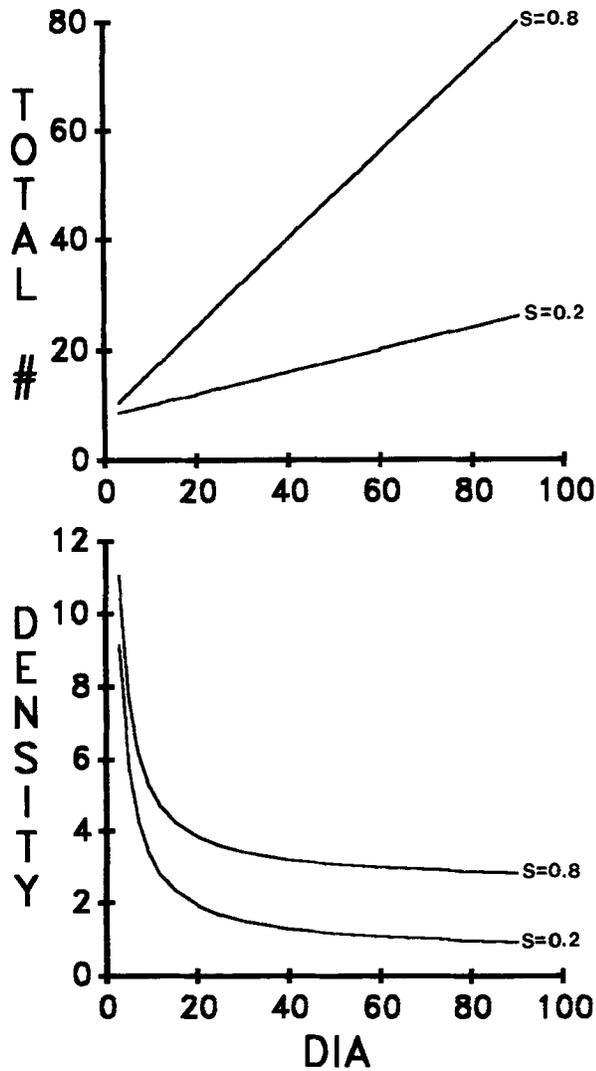


FIG. 3. Experimental relationship of slope of lines of equal intercept describing correlation between total number of an element and diameter in μm (DIA) to curves of element density (elements per $10 \mu\text{m}$ of circumference) versus diameter. Each element density curve is identified by the slope (s) of the corresponding total number line.

the $3\text{--}5 \mu\text{m}$ between strutted processes reported by Hasle and Fryxell (1977). Association of distance between strutted processes and diameter was not reported. However, most of the reported variation in distance between MSP in *T. conferta* is a curvilinear function of specimen diameter according to the results of this study (Fig. 5).

The *T. conferta* example may indicate why total number has not seemed to be a useful character; total number usually has a much greater absolute range of variation than does density (or distance). However, absolute range of variation has little to do with how well a character separates species because taxonomic utility is a function of both within and between taxon variation. Dividing total number of a rotational element by diameter will not appreciably reduce within taxon variation relative to among

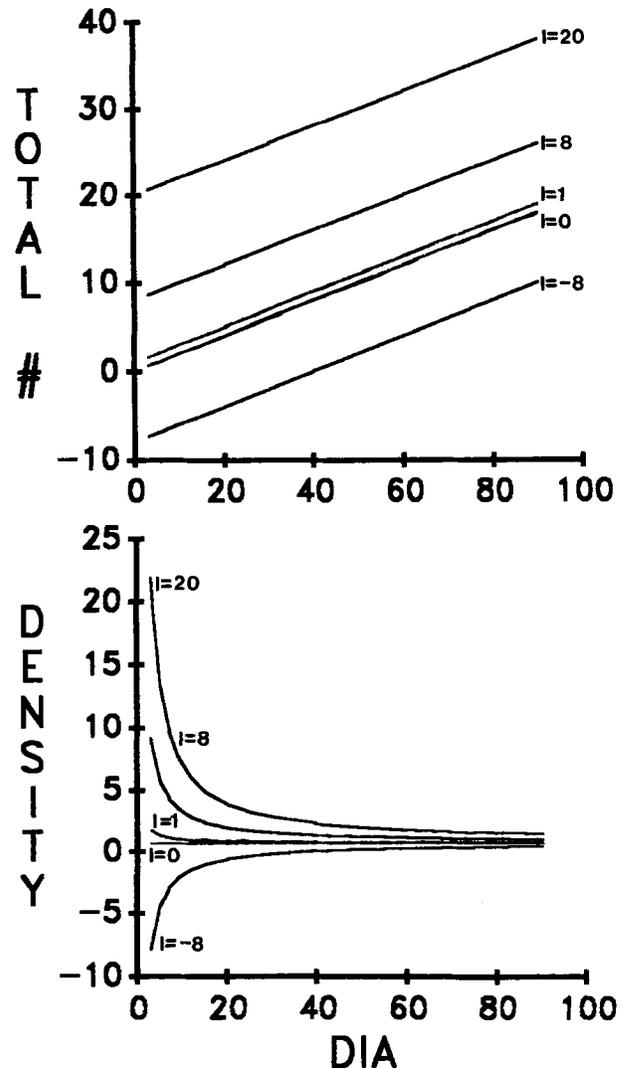


FIG. 4. Experimental relationship between intercept of lines of equal slope describing correlation between total number of an element and diameter in μm (DIA) to curves of element density (elements per $10 \mu\text{m}$ of circumference) versus diameter. Each element density curve is identified by the intercept (i) of the corresponding total number line.

taxon variation if the division does not remove within taxon dependence on diameter. Moreover, when curvilinearity is introduced to the density–diameter dependence, density actually becomes less useful than total number. For the qualitative taxonomist relying on “gestalt,” specimens of a species will look quite similar over a wide range of larger diameters, but smaller specimens will look increasingly more finely structured. This change happens quite rapidly over a relatively small range of diameters. The curvilinear relationship between density and diameter makes separation of species difficult even graphically (Fig. 6). In contrast, total number of elements versus diameter plots can provide the same degree of separation of species using a simple linear discriminator (Fig. 6).

Thus, diatom taxonomists should follow the ex-

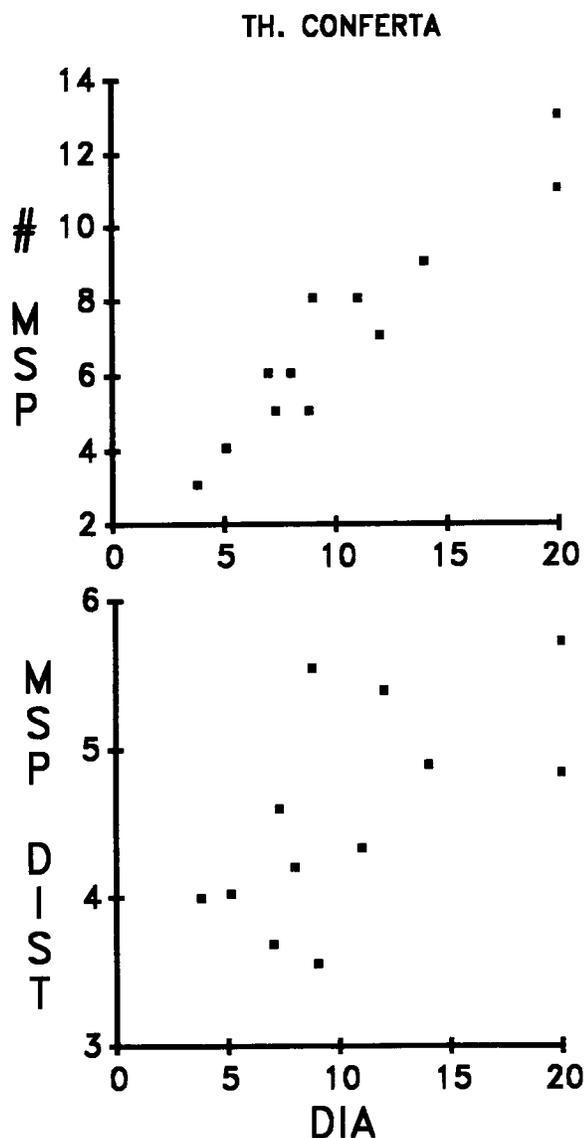


FIG. 5. Total number of marginal strutted processes (# MSP) and distance in μm between MSP (MSP DIST) versus diameter in μm (DIA) for *Thalassiosira conferta*.

amples of Genkal (1984) and Hickel and Håkansson (1987) and report the total number of an element and its relationship to diameter in taxonomic studies in addition to or instead of reports of density. If density is a taxonomically important character, plots of total number versus diameter will identify it as such, and it can then be applied in keys and descriptions. If density is treated without regard to its relationship to diameter, however, then any taxonomic information it may bear may be obscured in a comparison of two species of overlapping diameter. Conversely, consideration of density without recognizing its dependence on diameter (and that the degree of dependency is itself dependent on diameter) will likely lead to excessive splitting of species, especially those that span a size range of 3 to 20 μm , as smaller specimens will almost certainly look very much finer than larger specimens.

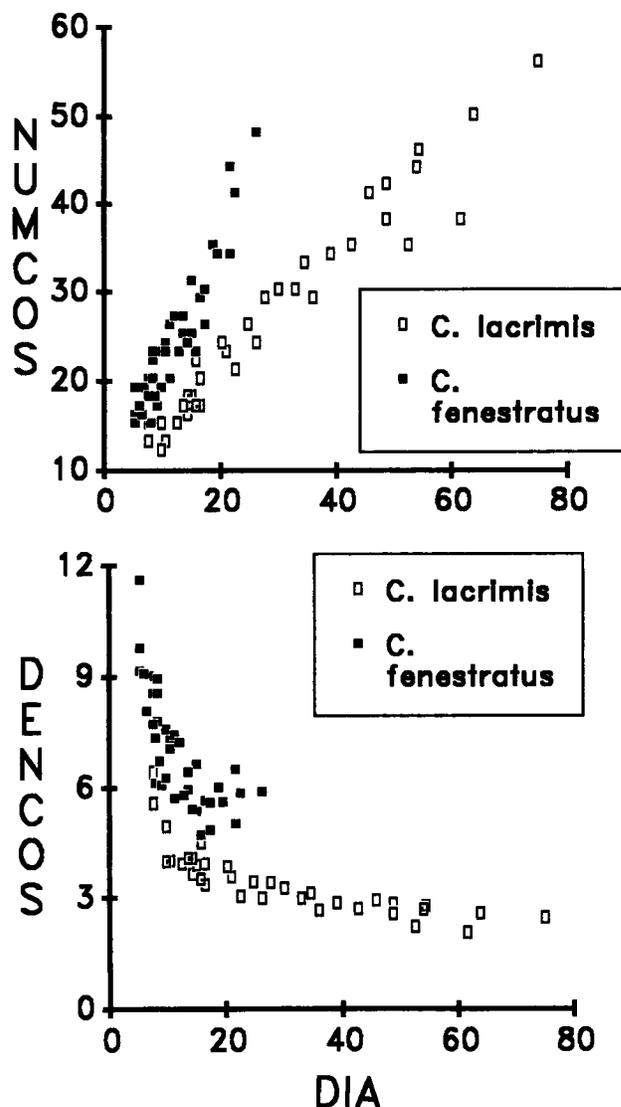


FIG. 6. Total number of costae (NUMCOS) and density of costae in 10 μm of circumference (DENCOS) versus diameter in μm (DIA) for *Cyclostephanos fenestratus* and *C. lacrimis* nom. prov. (Theriot and Bradbury, unpubl.). Note that similarity of shape but differences in altitude of the DENCOS curves correspond to the predictions of Figures 3 and 4 based on the species regression statistics for total number versus diameter (Table 1).

Other ratios in phycology. Rotational element density is a ratio of the number of elements to valve circumference. Difficulties of statistical behavior in density is but a special case of the more general problem of the use of ratios in morphometric studies. Bookstein et al. (1985) discussed the geometry of size-dependent and size-free shape variation and suggested that ratios are often employed to correct for real or imagined character interdependency, particularly to "adjust" shape for size, but will often fail to do so for a variety of reasons. In short, there are an infinite number of distance measures over the form of an organism. Ratios attempt to adjust for size by dividing the numerator by a denominator which is assumed to be a direct measure of size, or

at least closely related to it. It is unlikely that any one measure will directly correspond to size. Even if that measure (e.g. length, diameter or volume) corresponds closely to size, a curvilinear relationship between a ratio and its numerator or denominator might occur if variance in the numerator is dependent on the denominator. This paper illustrates the effect of a non-zero intercept of the numerator (total number) plotted against the denominator (diameter). Two ratios popular in phycoecology are not immune to these problems.

The most popular ratio in algal taxonomy involves length and width (as L/W or W/L). This ratio is often size dependent, compounding variation from several sources. In a recent non-diatom example, Baker (1987) found that L/W was exponentially related to W over a diversity of blue-green algae. Baker (1987) correctly suggested that the exponential relationship may be "a function of the mathematical relationship between the two variables," i.e. L and W, but did not identify the mathematical relationship. Visual inspection of Baker's data plots suggests that the curvilinear relationship between L/W and W actually has two components: non-zero intercept of L against W and correlation between L variance and absolute W value (as Baker reported, narrower cells are more variable in length). In contrast, most of the reported variation in L/W within a pennate diatom species is probably just a function of the intercept of L against W; one can verify this by plotting measurements of photographed specimens in Hostetter and Hoshaw (1972) and Tropper (1975).

Surface/volume (S/V) ratios are usually assumed to represent some morphological causal factor in physiological and ecological studies. Division by volume is an attempt to remove the effect of absolute size. An example of the confusion ratios can engender is an unresolved debate in the literature, based on the same data, about the relative contributions of size and shape on phytoplankton sinking rate. Smayda (1970:356-64) correlated sinking rate with $S (\mu\text{m}^2)/V (\mu\text{m}^3)$. He concluded that cell size influences sinking rate by "acting through the frictional drag in relation to the ratio of area to cell volume," implying that the ratio reflects allometry (i.e. the ratio being dependent on size) and not isometry (i.e. no corresponding change in the ratio with size) or shape differences independent of size (i.e. surface area differences among specimens with similar volume). Experience suggests that Smayda's S/V ratio probably does reflect allometry of size, but conclusive evidence is not available from Figures 3 and 4 in Smayda (1970). In fact, Vogel (1981:255) reanalyzed the data from Smayda's figures and reached a different conclusion (namely, that pure size is the main influence on sinking) using a somewhat different ratio. As part of his analysis, Vogel attempted to eliminate size by using a dimensionless ratio, $S^{1/2}/V^{1/3}$. However, this ratio is not necessarily independent of size even though it is dimensionless. For

example, it will be correlated with $V^{1/3}$ (and thus V) if $S^{1/2}$ plotted against $V^{1/3}$ has a non-zero intercept. Thus, with regards to the data in question, the potential correlation between size and the dimensionless ratio has not been conclusively disproven, nor has it been conclusively demonstrated that S/V is a measure of allometric shape. The question of relative contributions of size and shape to sinking in phytoplankton would still seem to require a definitive answer.

CONCLUSIONS

Ratios may be useful in limited circumstances. However, ratios are applied indiscriminately to problems in algal taxonomy, physiology and ecology. They are implicitly or explicitly used to correct for dependence of the numerator on the denominator but may fail to do so for a variety of reasons. Statistical interaction of the ratio with either the numerator or denominator can be even more complex than that between the original variables, as the experiments with fascicle density demonstrate. Thus, use of ratios is as likely to complicate description of morphology as it is to simplify it. Phycologists employing multivariate morphometric techniques to summarize algal size and shape should be especially cautious about using ratios because curvilinear relationships between morphological variables have the potential to introduce uninterpretable or artefactual dimensions just as curvilinear gradients can distort ecological ordinations (Noy-Meir and Austin 1970).

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