

Defensive spines: Inverse relationship between coefficients of variation and size¹

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Abstract

Coefficients of variation for spine lengths are not constant over a range of mean values, but show an inverse relationship with sample means. The nearly hyperbolic relationship is evident in selection experiments, in seasonal samples from a single lake, and in widely dispersed geographic samples. The observed inverse relationship could indicate an interesting developmental property (e.g. that smaller, rudimentary spines are more variable than larger functional ones) or could reflect one of several possible statistical artifacts or properties.

Detailed examination of *Bosmina* suggests that the strong inverse trend arises from a combination of biological and statistical properties; it is not an artifact of measurement error, although measurement error contributes to inflation of small values. Small spines are inherently more variable than longer spines, and the latter have more uniform component parts. Moreover, there are several alternative arrangements of components that sum to the same length and hence that achieve nearly equivalent fitness value. These alternative arrangements lower part-whole correlations within the population.

The two statistical properties that contribute to observed trends include a version of the central limit theorem and measurement error. The percentage variation of a character which is the sum of a number of randomly varying parts will be considerably less (roughly as the inverse square root of the number of parts) than the mean percentage variation of the parts themselves. Thus a statistical property of large numbers contributes to the observed inverse trend. In addition, coefficients of variation as fractions are especially sensitive to measurement error, so that precise measurements are recommended for small defensive spines.

Small planktonic organisms frequently carry spines or other forms of protection against larger bodied omnivorous or carnivorous invertebrates (Kerfoot 1980, 1987; Dodson 1984; Havel and Dodson 1984; Gilbert and Stemberger 1984; Stemberger and Gilbert 1987). This supplemental spinelike ornamentation is especially common in two freshwater taxa, cladocerans and rotifers, which propagate primarily by clonal reproduction. Whereas some of these protuberances aid evasion (e.g. the helmets of certain *Daphnia*: O'Brien and Vinyard 1978; Barry and Bayly 1985), most spinelike features hinder handling by consumers or directly prevent ingestion (Halbach 1971; Kerfoot 1978; Havel and Dodson 1984).

Typically, defensive spines are highly variable in space and time. Although some clones show little phenotypic variation from lake to lake and from season to season, many other, sometimes co-occurring, clones show

pronounced spatial and seasonal sensitivity to environmental cues (Hutchinson 1967; Kerfoot 1980; Barry and Bayly 1985). One possible explanation for phenotypic plasticity is that defensive structures are maintained at some cost to competitive prowess and other fitness demands (Kerfoot 1977; Reissen 1984). A general solution to the competitive dilemma is to evolve developmental flexibility. Under this solution, clones would produce antipredator defenses when and where risk is greatest. The alternative is to suffer great losses when predators are common or to bear needless expense when they are scarce. One of the more intriguing specific evolutionary adaptations of prey is predator-mediated chemical induction of defenses.

Chemical induction between predator and prey is widespread in certain taxa (recent reviews by Havel 1987; Harvel 1986). Acknowledged predator-prey induction pairs include a diversity of predators that influence cladoceran and rotifer spine lengths: *Asplanchna-Brachionus* (Gilbert 1966), *Anisops-Daphnia* (Grant and Bayly 1981),

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Chaoborus-Daphnia (Krueger and Dodson 1981), *Mesocyclops-Keratella* (Stemberger and Gilbert 1984), and *Epischura-Bosmina* (Kerfoot 1987). Additional freshwater examples are listed by Havel (1987).

Absolute lengths of mucrones and antennules in *Bosmina longirostris* are known to be associated with copepod predation. Mean lengths vary greatly geographically and seasonally, providing a large range of variation (Kerfoot 1980; Sprules et al. 1984). In general, long spines protect individuals, especially juveniles, from damage during handling by omnivorous and predatory copepods (Kerfoot 1975, 1978, 1987; Wong 1981*a,b*). A few clones of *Bosmina* show dramatic developmental elongation of features in the presence of predatory copepods (*Epischura*, *Mesocyclops*), with mucrones stimulated much more than antennules (Kerfoot 1987, unpubl. data).

Although spines can be developmentally fixed or chemically induced, maximum lengths usually coincide with close proximity to specific predators. For example, in the predatory copepod-*Bosmina* interaction, the spatial and temporal incidence of large spines closely matches the distribution and abundance patterns of highly efficient predators such as *Epischura* (Kerfoot 1975, 1980, 1987; Kerfoot and Peterson 1980; Sprules et al. 1984). Yet small protuberances are present in low-risk environments, with the spines diminished in size or modified in shape to blunt structures.

Most of the previous work has centered on the fitness relationships of mean spine length without consideration of variance, per se. However, my recent work has uncovered a strong pattern within data sets that treat the variability of defensive spines. Coefficients of variation for spine lengths are not constant over a range of mean values, but show an inverse relationship with sample means (Fig. 1). The relationship is evident in several types of descriptive data (e.g. geographic, seasonal, and enclosure studies) and poses some interpretive problems for more detailed quantitative genetic studies. The crucial question is whether the property arises as a real developmental or selected attribute, or is simply the consequence of statistical artifacts. If small spines are func-

tionless, vestigial structures, whereas large ones are subject to strong selection during active combat, strong stabilizing selection on large spines might favor greater developmental regulation. Alternatively, apparent reductions in developmental C.V. may arise from developmental correlation patterns (Pearson and Davin 1924; Lande 1977; Soule 1982) or from various statistical artifacts (Rohlf et al. 1983).

This contribution introduces the problem, examines departures from the two-parameter lognormal, an expected sampling distribution, and discusses options. The nature of the inverse relationship is examined, drawing almost exclusively from data on the small cladoceran *B. longirostris*.

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Materials and methods

Bosmina longirostris is a widely distributed, locally abundant, and parthenogenetic small cladoceran. Each individual possesses two paired spine-like extensions of the chitinous exoskeleton, the anterior antennules

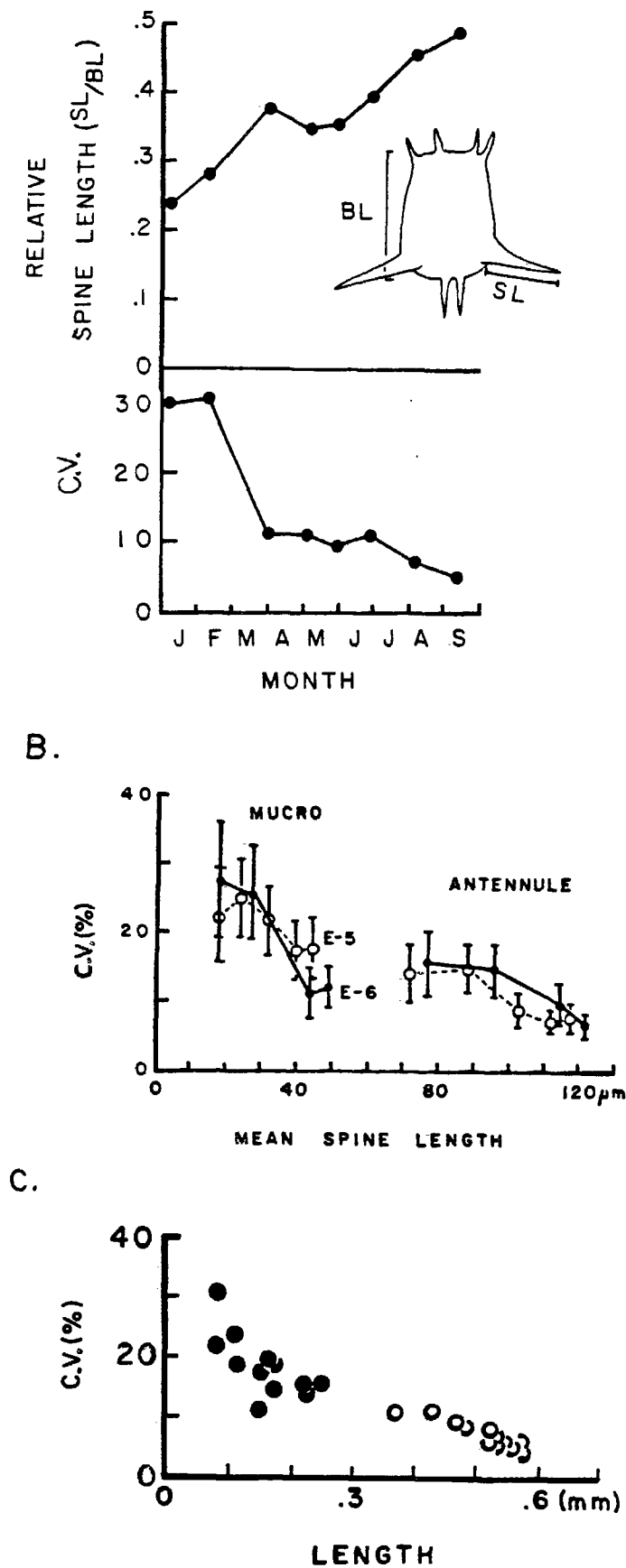


Fig. 1. Observed inverse relationship between spine length and sample C.V. A. Relative spine length and coefficients of variation for the rotifer *Brachionus* on several dates (SL—spine length; BL—body length). B. Mucro and antennule lengths of the cladoceran *Bosmina longirostris* (E-5, E-6 signify separate replicates; Kerfoot 1987). C. Helmet and tailspine lengths for a single size class (0.95 ± 0.025 mm) of *Daphnia galeata* (redrawn from Mort 1983).

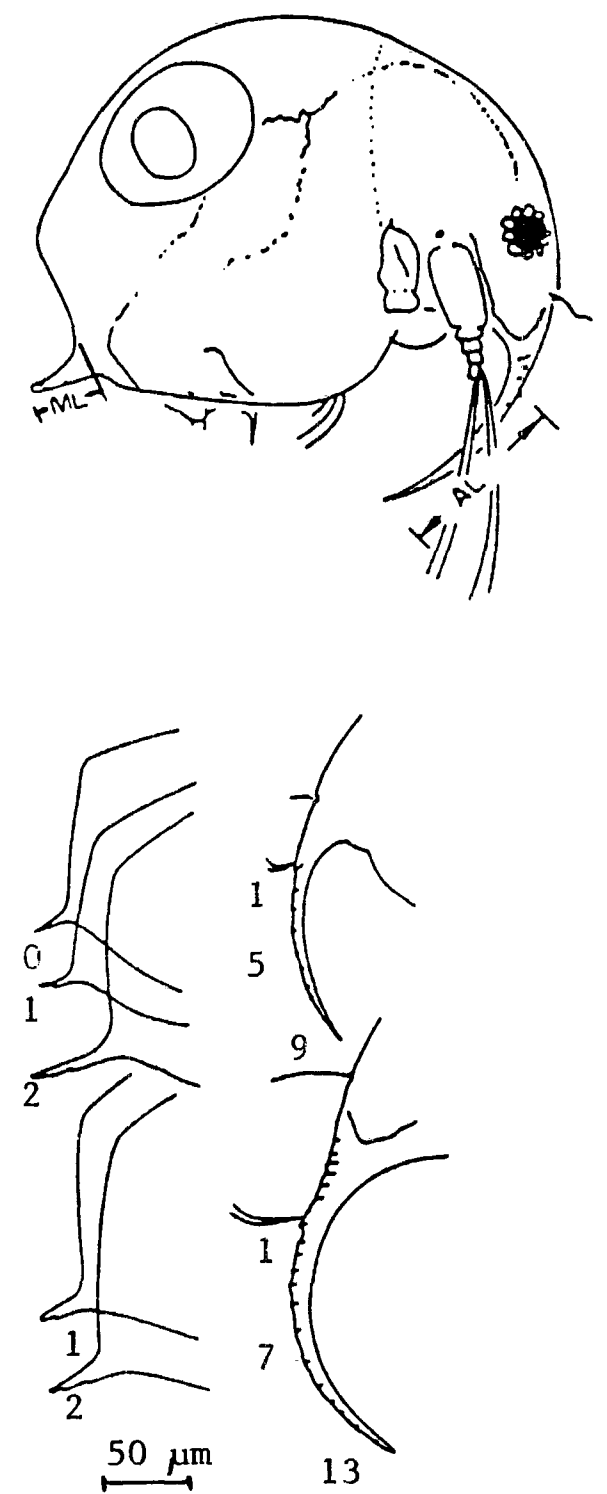


Fig. 2. Measurements on *Bosmina longirostris* (ML—mucro length; AL—antennule length; suture and segment counts shown for mucrones and antennules, respectively).

and the posterior mucrones (Fig. 2). Both defensive structures are usually at maximum length in first instars and show very little to no increase in absolute size in subsequent instars—a peculiarity that greatly simplifies ontogenetic considerations (Kerfoot 1975, 1980; Black 1980a,b). Mucrones and antennules are girdled at regular intervals by cell boundary marks (mucro sutures, antennule segments), allowing discrete

counts to be taken simultaneously with length measurements.

Length measurements are slightly different for the two structures (Fig. 2). For mucrones, lengths are measured from the distal tip to the base of the carapace along a straight line. For antennules, only the distal portion was measured, below the tooth-like projection which marks the insertion of the antennule setae (*see* Kerfoot 1975, 1980 for more details). Since antennules may be strongly curved or straight, length was measured along the outside curvature of the feature by rotating an ocular micrometer along the surface. Independent measurements were made on left and right pairs of these bilateral structures.

Coefficients of variation—The primary measure of morphological variation used here is the coefficient of variation or variability. This widely used measure is the sample standard deviation divided by the sample mean (C.V. = s/\bar{x}), often multiplied by 100 to express the fraction as a percentage of the mean value. The index was originally proposed by Karl Pearson in 1894 as part of a system of descriptive statistics in which the mean and standard deviation played prominent roles. More recently, especially in morphological studies, coefficients of variation have been used to remove scale effects. When homologous organs from different local populations or from different species are compared, empirical studies show that the C.V. is often much more invariant than either means, variances, or standard deviations (Haldane 1955; Wright 1968).

However, because the C.V. is a fraction that includes sample means, it is very sensitive to several kinds of statistical artifacts (Lande 1977; Rohlf et al. 1983). For example, if the standard deviation is constant, a plot of C.V. against the sample mean would simply be a plot of $1/\bar{x}$ against \bar{x} . If s and \bar{x} are bivariate normal and independent, then the inverse hyperbolic relationship would arise because a ratio is inversely correlated with its denominator (Atchley et al. 1976; Albrecht 1978; Rohlf et al. 1983). The observed decline would be hyperbolic, directly proportional to $1/\bar{x}$; or $1/\bar{n}$ if the measure were a count of equal-sized components (n). However, as pointed out by Rohlf et al.

(1983), in morphometric measurements s and \bar{x} are rarely independent; typically they are positively correlated with sampling distributions closely conforming to the bivariate lognormal (e.g. Wright 1968; Kerfoot and Kluge 1971).

Even when there is agreement with the lognormal, a second class of artifact can arise through measurement error. As in the paper of Rohlf et al. (1983), let us consider that a variable is lognormally distributed (with parameters μ and σ), that the measurement error is normally distributed (with parameters σ and σ_m), and that the measurements are grouped into classes of width w :

$$f_c(Y) = C \int_{-x}^x \frac{1}{(Y - X)} \cdot \exp \left\{ -\frac{1}{2} \left[\frac{\ln(Y - X) - \mu}{\sigma} \right]^2 \right\} \cdot \exp \left[-\frac{1}{2} \left(\frac{X}{\sigma_m} \right)^2 \right] dX. \quad (1)$$

Here the constant measurement error added to the system through instrument imprecision will cause $s = a + b\bar{x}$, where a comes from the added extrinsic error (Fig. 3A). Then C.V. = $(a + b\bar{x})/\bar{x}$, or C.V. = $a/\bar{x} + b$, which describes a decline to an asymptote (b) as $\bar{x} \rightarrow \infty$. Again the pattern is initially hyperbolic with C.V. $\propto 1/\bar{x}$ or $1/\bar{n}$. Rohlf et al. (1983) contended that the observed inverse relationship in most morphometric data sets arises from either measurement error, in the case of continuous variates, or from "grouping error" in the case of discrete variates. To support their concern, Rohlf et al. (1983) presented a series of simulation results. However, to achieve reasonable fit, these simulations required nearly 20% measurement error to match observed trends in morphometric variables. This seems unreasonable and suggests that some as yet undisclosed process is important in producing the pattern. Regardless, one simplifying aspect is apparent in defensive spines. Since all the *Bosmina* measurements and counts are linear, questions of dimensionality are not of concern (Lande 1977).

Characteristics of the lognormal—Evaluation of statistical properties requires knowledge of sampling distributions. The

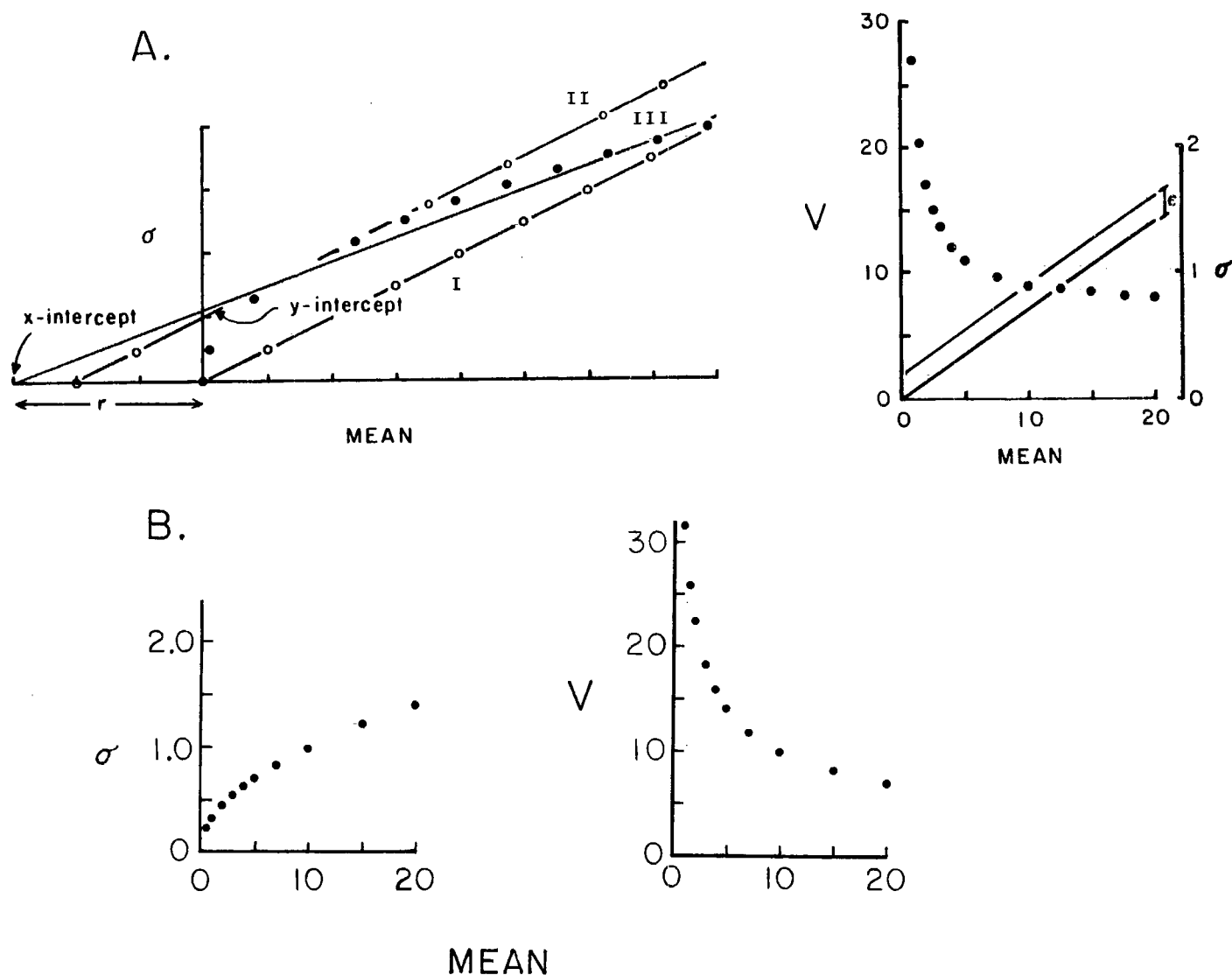


Fig. 3. Hyperbolic patterns that arise from measurement error or large number properties. A. Case I—simple two-parameter lognormal; case II—simple two-parameter lognormal pattern plus constant measurement error, showing positive y -intercept (specific example to right, intrinsic $V = 7\%$, $SD = 1.4$, measurement error = 0.2); and case III—positive y -intercept caused by fitting linear regression to Pearson-Davin pattern. B. Example of Pearson-Davin property discussed in text.

most common intuitive appeal of the C.V. is that it removes scaling effects, an attribute recognized as valuable for comparison studies of animal morphology (in particular, Simpson et al. 1960).

Proportional variation of the mean and standard deviation is common and forms the basis of the two-parameter lognormal distribution; that is, the distribution arises from the so-called law of proportionate effect. A variable is said to obey the law of proportionate effect if the change in the variable at any step is a random proportion of its previous value (Aitchison and Brown 1966), i.e. if

$$X_j - X_{j-1} = \epsilon_j(X_{j-1}), \quad (2)$$

where the set $[\epsilon_j]$ is mutually independent and also independent of the set $[X_j]$.

The lognormal distribution in its simplest form, i.e. the two-parameter case, is defined as the distribution of a variate whose logarithm obeys the normal law of probability. To distinguish the properties of a lognormally distributed variable from those of its normally distributed logarithmic transformation, I follow the notation of Aitchison and Brown (1966). A positive variate X ($0 < x < \infty$) is lognormally distributed in the two-parameter case if $Y = \log X$ is normally distributed with mean μ and variance σ^2 . Because $Y = \log X$ is not defined for $X = 0$, X cannot assume 0 values, although in practice this liability is often overcome by adding a positive number, e.g. $Y_i = \log(X + 1)$. The j th moment about the origin (λ_j) is

$$\lambda_j = \exp(j\mu + \frac{1}{2}j^2\sigma^2) \quad (3)$$

from the properties of the moment-generating function of the normal distribution. The mean (α , first moment) and variance (β^2 , second moment) of the lognormal distribution are then

$$\alpha = \exp(\mu + \frac{1}{2}\sigma^2) \quad (4)$$

and

$$\begin{aligned} \beta^2 &= \exp(2\mu + \sigma^2)\exp(\sigma^2 - 1) \\ &= \alpha^2 V^2 \end{aligned} \quad (5)$$

where

$$V^2 = \exp(\sigma^2 - 1). \quad (6)$$

The standard deviation $\beta = \alpha V$, and $V = \beta/\alpha$; hence the two-parameter lognormal distribution describes a linear relationship with slope β/α between the parametric standard deviation (β) and mean (α) with a zero intercept (Fig. 3A). The coefficient of variability is a parameter (V) estimated by a sample statistic, here termed the coefficient of variation (C.V.) to separate parametric values from sample statistics.

Lognormal with measurement error—Modification of the two-parameter lognormal permits incorporation of measurement error. In terms of geometry, the problem involves a simple translation of the two-parameter case (cf. cases I and II, Fig. 3A). The intercept on the y -axis represents the additive contribution of measurement error to the observed standard deviation.

For correction of measurement error, a direct method is simply to subtract the Gaussian measurement error component from the total variance. This approach is recommended over the estimation of negative x -intercepts (e.g. Aitchison and Brown 1966; Kleczkowski 1949).

Confidence limits—For field samples, confidence limits around coefficients were determined by the following formula for the standard error of the C.V.:

$$S_{c.v.} = \frac{C.V.}{(2n)^{1/2}} \left[1 + 2 \left(\frac{C.V.}{100} \right)^2 \right]^{1/2} \quad (7)$$

(Sokal and Rohlf 1981). Note that this formula is only an approximation, since it assumes a normal distribution. However, agreement is usually very good for low coefficients of variation (Wright 1968). Care was also taken to avoid very small sample sizes,

since these will also bias the C.V. (Haldane 1955).

Measurements and measurement errors—Continuous (length) and discrete (mucro sutures, antennule segment counts) measurements were recorded from *Bosmina*. Routine length measurements were made at 500 \times magnification under a Zeiss Universal compound microscope, on glycerin-water (50%–50% mixture) mounted individuals. Sample sizes for seasonal samples were usually fixed at $n = 40$; mean values and 95% C.L. were graphed by Kerfoot (1987, figure 2). Sample sizes for most geographic samples were also fixed at $n = 40$ (range 18–89, mean 40.1). Under these conditions, measurement error comes from three primary sources: instrument precision (fineness of the ocular micrometer scale, magnification and optical resolution of the microscope at 500 \times), preparation error (specimen orientation between cover slip and slide), and observer error.

For the *Bosmina* set, the importance of measurement error in continuous characters was estimated through direct measurement (i.e. repeated measurement of specimens) and indirectly by varying instrument precision. The ocular micrometer scale used for length measurements had a basic resolution interval of 1.6 μm at 500 \times , with interpolation possible between marks. In the precision test, a short-mucroned, high C.V. sample (Occom Pond) of 40 individuals was measured under the Zeiss Universal at different magnifications (200–800 \times). If a high C.V. at 500 \times is solely an artifact of measurement error, then lowering the magnification should increase the C.V. because relative measurement error is increased; while, conversely, increasing the magnification should decrease the C.V. because measurement becomes more precise.

For meristic (countable) characters such as segment or suture counts, there are additional, complicating problems. Inflation of the C.V. may result from the presence of zero values (Wright 1968; Lande 1977) or grouping effects (Thompson 1950, 1951; Aitchison and Brown 1966). The problem of truncation and zero values in *Bosmina* meristic variables is treated simply by indicating the mean value below which zeros appear in calculated sample estimates. The

difficulty with grouping arises because discrete distributions only approximate the theoretical continuous condition of either the normal or lognormal distribution, requiring adjustment analogous to Sheppard's correction for grouping error in a discrete normal approximation. Unfortunately, the lognormal approximation is complicated by two conditions (grouping in unequal intervals, lack of high contact near the origin in cases of truncation) that violate the Euler-MacLaurin formula on which Sheppard's correction depends (Thompson 1951). Rohlf et al. (1983) used simulation studies to solve for particular values, apparently unaware that Thompson (1951) had previously published tabled corrections for "Sheppard-like" effects in the discretized lognormal. Assessment of the "grouping" artifact goes beyond the scope of this paper. However, comparison of coefficients of variation for continuous (length) and discrete (mucro sutures, antennule segment counts) measurements contrast patterns for the two variables.

Regression analysis—Regression analysis (BMD Statistical Package, Univ. Mich. Amdahl 470) was applied to most standard deviation/mean plots. The exercise was intended to check for linearity of patterns near the origin and for estimation of x - and y -intercepts (Kleczkowski 1949; Aitchison and Brown 1966). Plots of C.V. used either single sample coefficients of variation or, in the case of multiple estimates, mean coefficients of variation (\bar{V}) for reasons cited in Rohlf et al. (1983). Regression plots for multiple samples used mean sample standard deviations (\bar{s}). Regressions were also inspected for heteroskedasticity (a feature characteristic of lognormal plots) and for systematic deviations from linearity.

Between-individual and within-individual measures—Another simple test involved between-individual and within-individual components of total variance. A real increase in relative variance over time could relate either to polymorphisms or to developmental timing effects during induction. That is, after an episode of spine induction, the between-individual component might contribute the majority of variation, while the within-individual component (e.g. left-

right asymmetry) might remain much more conservative. To test this property, I calculated two measures of bilateral asymmetry: Soule's (1967) index of fluctuating asymmetry and an ANOVA estimate of within-individual variance. Soule's (1967) index of asymmetry ($d = \Sigma |l| - |r|$) was calculated for left (l) and right (r) mucro and antennule pairs. However, this index has several undesirable features and is really just a two-point estimate of the within-individual range. Hence, it will be correlated with, yet larger than, an estimate of the within-individual standard deviation for the same character. A much more direct and desirable approach used ANOVA techniques.

The ANOVA estimate of within-individual "developmental noise" is equivalent to the special environmental variance component of Falconer (1981). Paired, bilateral measurements (i.e. left- and right-hand side lengths, counts) were treated as replicate measurements in a nested single classification ANOVA scheme (Palmer and Strobeck 1986). For a sample size of 40, each individual provided a two-point estimate of the within-individual standard deviation ($2 \times 40 = 80$ measurements).

Component-whole considerations (Pearson-Davin argument)—An alternative argument for the origin of hyperbolic patterns was offered initially by Pearson and Davin (1924) and more recently by Lande (1977) and Soule (1982). This argument constitutes a form of null model, since it illustrates how a marked decline in C.V. can arise from random variation of components.

Lande's (1977) argument considered the comparison of the C.V. of a whole to that of its parts. This argument is appropriate for linear structures, like defensive spines, that are composed of an increasing number of cells (segments, suture boundaries). Here, the whole is expressed as the sum of n parts,

$$S = \sum_{i=1}^n X_i. \quad (8)$$

Therefore $\sigma_{s^2} = \sum_{i=1}^n \sum_{j=1}^n r_{ij} \sigma_i \sigma_j$ and the C.V. of the whole is

$$V_s = \left(\sum_{i=1}^n \sum_{j=1}^n r_{ij} \mu_i V_i \mu_j V_j \right)^{1/2} \div \sum_{i=1}^n \mu_i \quad (9)$$

Lande noted that only in the extreme case when the variation of all parts is perfectly correlated (i.e. $r = 1.0$), the C.V. of the sum attains its maximum value, identical to the average V_i of its parts, weighted by their means

$$V_s \leq \sum_{i=1}^n \mu_i V_i \div \sum_{i=1}^n \mu_i \quad (10)$$

Thus the V for a composite measure that shows less than perfect correlation of components would always be less than the weighted average of the V_s for its parts. If variation in the components is completely independent, a composite structure of n identical components (V_i), each with a mean μ and a variance σ^2 , would have a C.V. of

$$V_s = (n\sigma^2)^{1/2} n\mu = n^{-1/2} \sigma / \mu \quad (11)$$

with V_s proportional to $n^{-1/2}$ (Lande 1977; Soule 1982).

The contrast between poorly and moderately correlated components can be dramatic. If components are perfectly correlated, V_s remains constant with increasing number of components, while σ increases directly with n as a simple scaling argument. However, reduction in correlation results in substantial drops for V_s , with the rate of decline most notable near the origin (Fig. 3B). If the components vary independently, V_s declines dramatically as an inverse square-root function of n , while σ increases gradually as a positive square-root function of n . For example, Fig. 3B illustrates how parameters change with n , the number of components, as a function of component correlation. Here $V_s = 10\%$ at $n = 10$, with a component $V_c = 0.316$ (i.e. at $n = 1$, C.V._s and C.V._c would be equivalent). If there is no component correlation, V_s declines hyperbolically from its component value ($V_s = 0.316 n^{-1/2}$), whereas σ increases more gradually ($\sigma = 0.316 n^{-1/2}$), both parameters

changing 6.7-fold over the range (i.e. 1–45) relative to initial values.

Note how the increase in σ becomes nearly linear at high values and with increased correlation of components. If a linear regression equation were fit to observed values removed from the origin, one would also obtain an imaginary positive intercept on the y -axis at the origin (Fig. 3A; case III). The y -intercept would approach the origin only in cases of high component correlation.

Results

Inverse relationship between coefficients of variation and sample means—All of the data sets for defensive structures examined thus far show an inverse relationship between C.V. and sample mean. These trends are especially pronounced in defensive spines of rotifers and cladocerans and can be illustrated by three examples (Fig. 1). The first example (Fig. 1A) treats interactions between a predatory rotifer, *Asplanchna brightwelli*, and the small, herbivorous rotifer *Brachionus calyciflorus* (Halbach and Jacobs 1971). *Asplanchna* both selectively removed short-spined individuals and induced longer spines in *Brachionus*, while prey body length remained relatively unaffected. The figure gives spine lengths obtained from a standard laboratory procedure designed to correct for induction. In the assay, field samples were placed in a known concentration of *Asplanchna*-substance, measured after induction, then the mean lengths plotted vs. the time of sampling. Field populations showed a progressive increase in mean spine length and a corresponding reduction in C.V. The increase in mean spine length was attributed to directional selection, whereas the decline in C.V. was interpreted as a consequence of truncation during directional selection (Halbach and Jacobs 1971).

The second example (Fig. 1B) involves selection by the predatory copepod *Epiischura lacustris* for increased spine length in the small cladoceran *B. longirostris* (Kerfoot 1987). In these enclosure studies, the C.V. for mucro and antennule lengths declined significantly in the presence of *Epiischura* as features moved toward greater

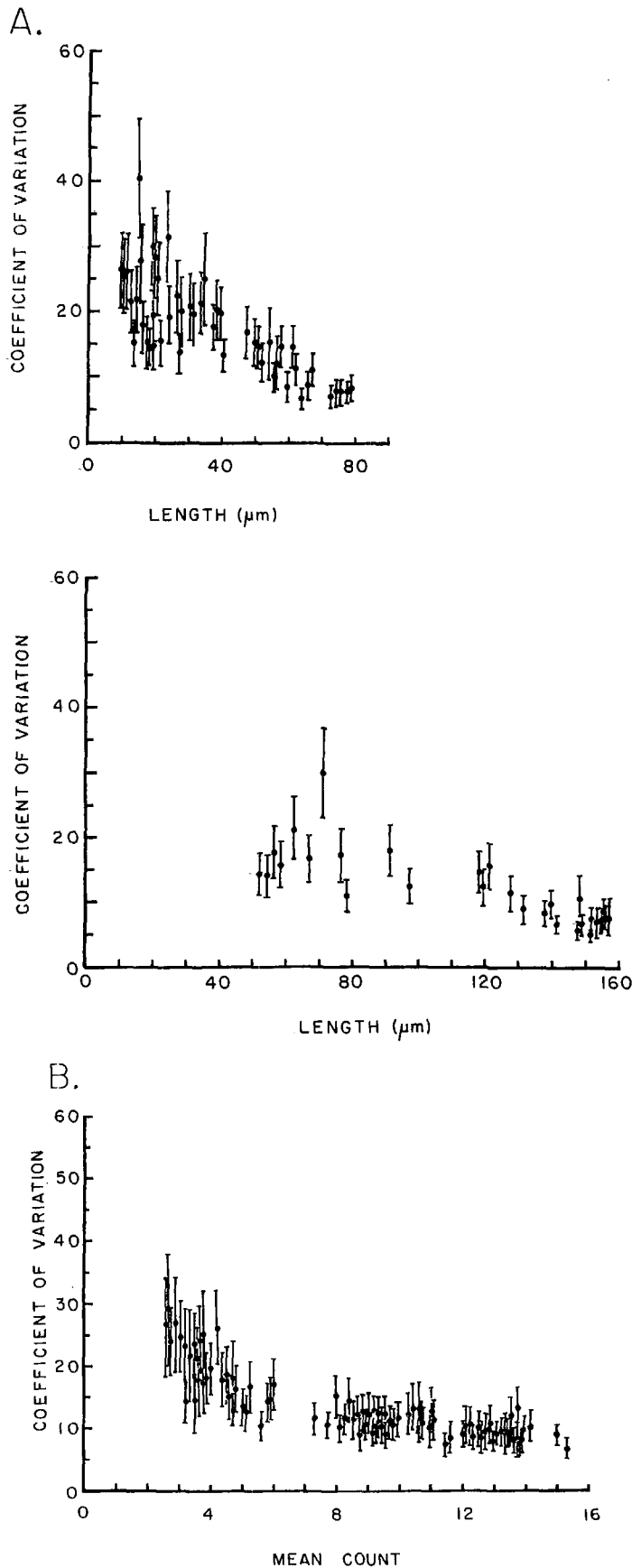


Fig. 4. Inverse relationship between C.V. and feature size for seasonal samples. A. Mucro and antennule lengths plotted separately. B. Mucro suture and antennule segment counts plotted on same graph (2-6, sutures; 7-16, segments). Suture coefficients of variation below a value of 2 are not plotted, as these data contain zeroes (truncation effects). Vertical lines indicate 95% C.L.

mean lengths. As in the previous example, both directional selection and developmental induction were presumed responsible for mean spine length shifts. The reduction in C.V. was attributed to truncation during directional selection (Kerfoot 1987).

The third and final example is taken from a study of helmet and tailspine variation in *Daphnia galeata*, a moderate-sized herbivorous cladoceran (Fig. 1C). At the study site in Lake Morey, Vermont, *D. galeata* underwent considerable seasonal variation in helmet and spine lengths (Mort 1983). Here the allometric growth of features introduced complications. However, if coefficients of variation for a single, restricted size class of juveniles (0.95 ± 0.025 mm) are plotted vs. protuberance lengths, there is again a clear inverse relationship. In this study, the predators associated with fitness shifts in spine and helmet lengths were not clearly identified, although indications pointed toward *Chaoborus punctipennis* (Mort 1983, 1986).

All three examples of inverse relationships might be attributable either to truncation during natural selection for increased spine lengths or to increased stabilizing selection on larger features, both of which are interesting biological phenomena. Yet, there may be alternative explanations, ones which involve statistical properties. In the case of *Bosmina*, highly significant inverse relationships between C.V. and sample mean also are evident in routine seasonal samples from a suite of New England lakes and from broad geographic surveys.

Seasonal samples—Seasonal samples from three New England lakes (Occom Pond, Lake Mitchell, Lake Norford; see Kerfoot 1987) show an almost hyperbolic inverse relationship between C.V. and size. Coefficients of variation for mucro lengths and suture counts show a more pronounced inverse relationship and are higher than the corresponding measurements on antennules (Fig. 4). When the data are arranged by absolute mean count, the count set reveals a much more orderly transition between mucro and antennule values, whereas the length set shows that the C.V. is distinctly elevated at small values for both features. There is also evidence for seasonal

heterogeneity, as samples with nearly identical means may have significantly different coefficients of variation (Fig. 4A).

Increased coefficients of variation at small absolute lengths of mucrones and antennules correspond to noticeable differences in the shape of features between individuals, especially in the case of antennules where there is polymorphism. Short-antennuled individuals may fall into either strongly "hooked" categories (the "curvirostris" form of Herbst 1962; the "cornuta" form of Brooks 1957) or more gently curved categories (the "brevirostris" forms of Herbst 1962; the typical form of Brooks 1957). Expression of these alternative phenotypes is modified by ontogeny, for all individuals possess gently curved antennules in the first two immature instars and only show "hooked," "straight," or gently curved forms in the third and later mature instars. Corresponding shape variations in mucrones are not as pronounced, yet phenotypes range from blunt, nublike categories to straight, spinelike forms (Fig. 2).

Geographic samples—Mean coefficients of variation for widely ranging geographic samples also show patterns nearly identical to those evident in the more restricted seasonal set (Fig. 5, Table 1). Again the inverse relationship between C.V. and sample mean is more striking for mucrones than for antennules. The two independent measurements (lengths, counts) basically show similar patterns, yet again the count data show a smoother transition with increasing scale, whereas the length data emphasize increased coefficients of variation of both small mucrones and small antennules above overall trends.

Mean values of C.V.s for small mucrones are also much higher than the corresponding values for small antennules. Mean values of C.V. for small mucrones show greater scatter of individual values around class means (Table 1). Increased scatter is expected for two reasons: scatter of individual estimates around class means is expected to be proportional to the mean C.V. (Eq. 7), and point estimates fall along the region of steepest decline in the hyperbolic relationship of C.V. to sample mean. Scatter of point

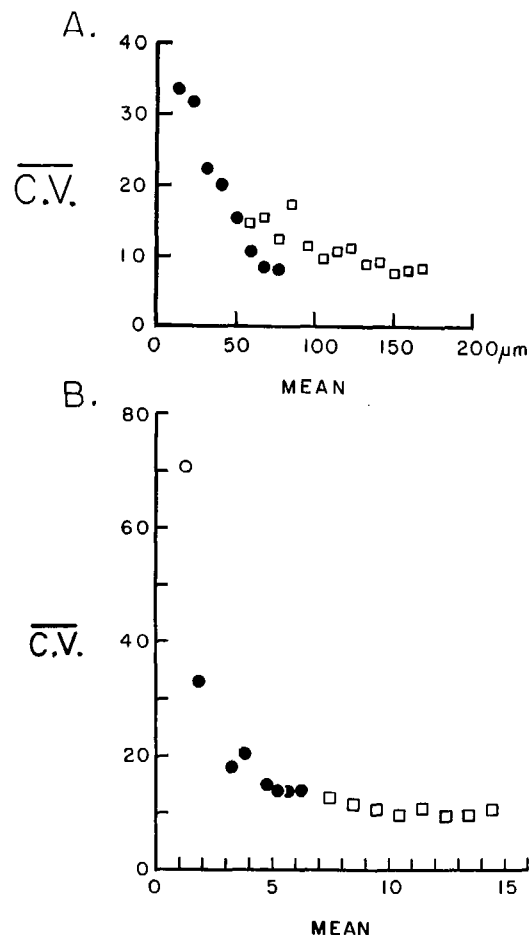


Fig. 5. Inverse relationship between C.V. and feature size in geographic samples. A. Mucrones (●) and antennules (□) of different mean lengths. B. Mucro suture (●) and antennule segment (□) counts.

estimates about mean values is indicated by standard deviations in Table 1. These values show a marked decline as sample mean counts or lengths increase. The extremely high absolute values of C.V. in mucro counts are attributable to statistical truncation effects (presence of zeros; see *materials and methods*).

Regression analysis—Since the C.V. is a quotient, it is important to inspect numerator behavior independent of denominator values. Moreover, trends in sample standard deviations across different mean values check agreement with suspected sampling distributions (see *materials and methods*). Recall that a positive linear increase is expected in the case of the simple two-parameter lognormal distribution.

Overall results of regression analysis on seasonal and geographic data sets were similar (Fig. 6, Table 2). In the seasonal set, regressions of sample standard deviations on sample means gave highly significant,

Table 1. Patterns in geographic survey data: mean coefficients of variation, mean standard deviations, sites, and sizes of samples. Site designations are Frains Lake, Michigan (F); Michigan lakes survey (MS); Occom Pond, New Hampshire (O); Lake Mitchell, Vermont (M); Lake Norford, Vermont (N); and Lake Washington, Washington (W). Number of samples indicated under *N*; sample sizes—40 individuals, or between 3,500–4,000 individuals per variable.

Length (μm)	Site	<i>N</i>	C.V. (SD)	$\bar{S}\bar{D}$	Count*	Site	<i>N</i>	C.V. (SD)	$\bar{S}\bar{D}$
Mucrones									
11.0–20.1	O, W	19	33.5(10.9)	0.27	0.0–0.5	F	6	152.7(31.6)	0.38
20.1–27.5	O, W	10	31.8(7.0)	0.41	0.6–1.0	F	17	111.7(25.7)	0.89
27.5–38.4	F, MS	17	22.2(5.5)	0.40	1.1–1.5	F	12	70.8(20.5)	0.89
38.4–45.8	F, M	11	20.2(5.5)	0.47	1.6–2.0	F	10	32.9(4.6)	0.59
45.8–56.7	MS, M, N	8	15.6(4.2)	0.44	3.0–3.5	M, N	5	20.0(5.1)	0.59
56.7–65.9	MS, M, N	10	10.7(3.1)	0.35	3.5–4.0	M	5	20.2(2.9)	0.76
65.9–75.0	MS, N	5	8.5(1.6)	0.32	4.5–5.0	M	3	15.2(1.9)	0.72
75.0–82.4	N	4	8.2(0.5)	0.35	5.0–5.5	N	9	15.3(2.2)	0.79
					5.5–6.0	N, W	15	15.3(2.6)	0.87
					6.0–6.5	W	14	14.3(1.5)	0.90
Antennules									
54.9–65.9	O, W	12	14.9(3.0)	0.49	7.1–8.0	O	3	12.7(2.3)	0.99
65.9–75.0	O, W	12	15.4(6.0)	0.59	8.1–9.0	O	6	11.7(2.0)	1.03
75.0–84.2	O, W	7	12.4(2.8)	0.53	9.1–10.0	F, O, W	36	10.8(3.5)	1.04
84.2–93.3	MS, O, W	4	17.3(5.6)	0.83	10.1–11.0	F, W	57	9.9(1.7)	1.05
93.3–102.5	F, O, MS, W	4	11.4(1.0)	0.60	11.1–12.0	F, M, W	30	11.0(2.5)	1.28
102.5–111.6	F, MS	10	9.7(3.6)	0.56	12.1–13.0	F, M, N	9	9.7(1.4)	1.22
111.6–120.8	F, N	7	10.6(2.5)	0.67	13.1–14.0	M, N	13	9.9(1.8)	1.35
120.8–129.9	F, MS, N	4	11.1(3.1)	0.76	14.1–15.0	F, M, N	4	10.8(1.3)	1.58
129.9–139.1	F, N	4	8.9(0.7)	0.65					
139.1–148.2	F, M, N	5	9.2(3.0)	0.72					
148.2–157.4	F, M, N, MS	14	7.6(1.4)	0.63					
157.4–166.5	M, N, MS	4	8.1(1.0)	0.71					
166.5–173.9	N	4	8.4(1.1)	0.78					

* Mucrones—sutures; antennules—segments.

positive slopes for three separate variables: mucro lengths ($r^2 = 0.419$), mucro sutures ($r^2 = 0.812$), and antennule segments ($r^2 = 0.379$). Trends for antennule lengths were not significant ($r^2 = 0.000$), because of high standard deviations at low mean values (i.e. the polymorphism mentioned earlier). If either the combined length data or count data are plotted against increasing scale, overall trends with increasing mean values are positive and highly significant (lengths, $r^2 = 0.416$; counts, $r^2 = 0.810$; Table 2). Comparable regressions for mean standard deviations in the geographic set gave highly significant, positive slopes for antennule segments ($r^2 = 0.854$) and lengths ($r^2 = 0.325$), but positive, nonsignificant slopes for mucrone lengths ($r^2 = 0.002$) and sutures ($r^2 = 0.205$, Table 2). When combined length or count data were plotted against increasing scale, the overall trends were again positive and highly significant (length $r^2 = 0.627$; counts $r^2 = 0.803$).

One feature of regressions was pro-

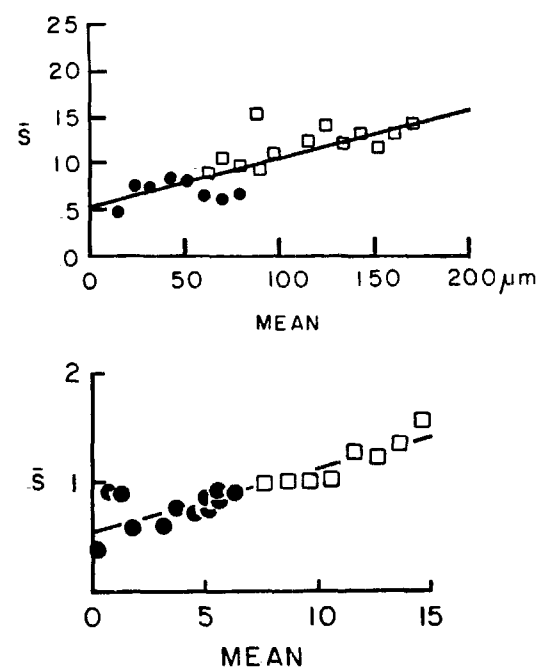


Fig. 6. Regression of average standard deviations on sample means for the geographic set (Table 2 gives separate and combined regressions). Note the apparent imaginary positive y -intercept. Symbols as in Fig. 5; upper panel—lengths; lower panel—suture or segment counts.

Table 2. Regression of sample standard deviations on sample means. Results separated into two categories: individual features and combined length or count variables. Other information includes sample size (N), F -value for regression and significance (P_1), T -value for SD-intercept, and significance (P_2).

	N	Regression equation	F	P_1	T	P_2
Individual feature						
Seasonal						
Mucro length	33	SD = 0.0507 X + 3.26	22.4	0.0000	5.9	0.0000
Mucro sutures	33	SD = 0.1398 X + 0.13	134.1	0.0000	3.0	0.0058
Antennule length	33	SD = -0.0017 X + 12.79	0.0	0.9242	6.0	0.0000
Antennule segments	33	SD = 0.0524 X + 0.57	18.9	0.0001	3.9	0.0004
Geographic						
Mucro length	8	SD = -0.0001 X + 0.38	0.0	0.9117	6.2	0.0008
Mucro sutures	10	SD = 0.0358 X + 0.62	2.1	0.1884	6.4	0.0002
Antennule length	13	SD = 0.0016 X + 0.47	5.3	0.0418	5.4	0.0002
Antennule segments	8	SD = 0.0774 X + 0.34	35.2	0.0010	2.3	0.0587
Combined feature						
Seasonal						
Length	66	SD = 0.0619 X + 4.07	45.6	0.0000	4.7	0.0000
Count	66	SD = 0.0781 X + 0.28	272.5	0.0000	6.8	0.0000
Geographic						
Length	21	SD = 0.0520 X + 0.30	32.8	0.0000	6.0	0.0000
Count	18	SD = 0.0585 X + 0.55	65.3	0.0000	9.3	0.0000

nounced. All regressions had positive intercepts on the y -axis (SD) and consequently had slopes less than the observed mean coefficients of variation (Table 2; Fig. 6). In the seasonal set, slopes $\pm 95\%$ C.L. were: lengths 0.062 ± 0.009 , counts 0.078 ± 0.005 ; in the geographic set they were: lengths 0.052 ± 0.018 , counts 0.058 ± 0.007 . The positive intercepts were significant to highly significant (Table 2). Thus both lengths and counts show a positive relationship between sample standard deviations and means, yet the positive intercepts on the y -axis and the disagreement between regression slopes and coefficients of variation show that the simple, two-parameter lognormal model does not fit (see materials and methods). Such apparent positive intercepts for SD values at zero mean values are a consequence either of legitimate increases in inherent variation of smaller features, statistical properties mentioned earlier (component-whole considerations), or measurement error.

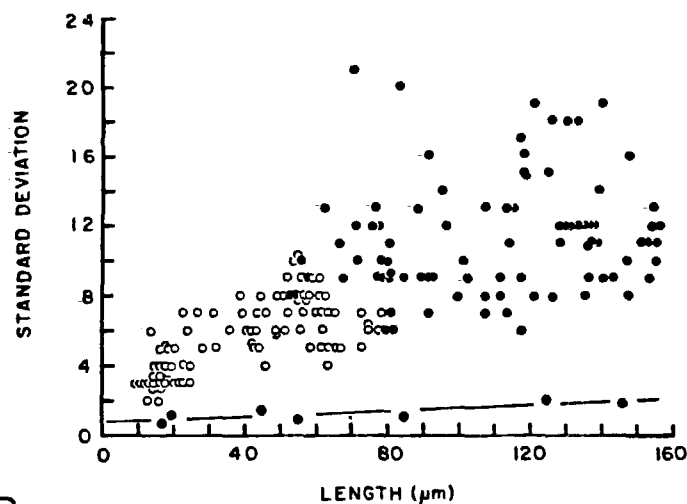
Measurement errors—Direct estimates of measurement error, based on multiple measurements over a wide range of spine lengths, gave average SD values between 0.6 and 1.9 μm (Fig. 7A). The values showed a slight increase with absolute feature length. For antennules and for long mucrones, the contribution to total variance is minor (long

antennules, 1–4%; short antennules, 1–3%; long mucrones 1–4%), but can be moderate for the smallest mucrones (3–25%, average $\sim 8\%$ of the total variance).

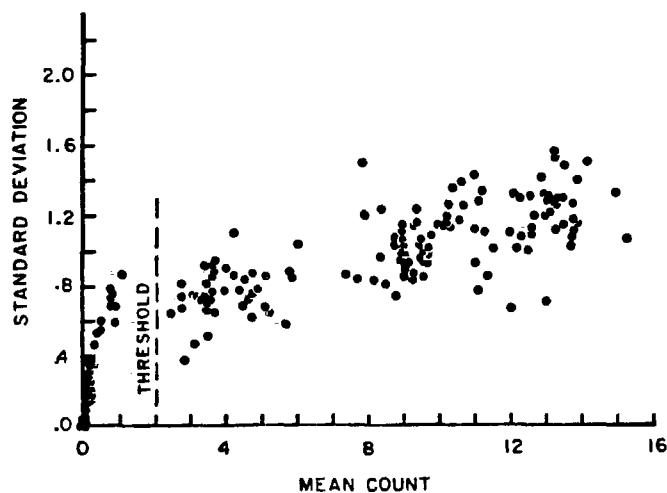
Varying magnification on a 20- μm spine sample (Occom Pond) did not have a major effect on the observed C.V. value. The decline was only $\sim 11\%$ over the magnification range (200–800 \times) and not significant (Table 3). Thus direct estimates of measurement error and instrument precision tests indicate that the major inflation of the C.V. (4 \times) for small spine lengths is real and that most of the inflation is not attributable to measurement error.

Within-individual and between-individual contributions—Within-individual variation (Fig. 7C) increased with an increasing mean, although values were small and the relationship was more linear. The ANOVA estimates for SDs were less than the value for the Soule index because, as mentioned earlier (materials and methods), the Soule index is essentially a two-point estimate of the range, rather than the standard deviation. The importance of a direct estimation of the within-individual component is the clear demonstration that absolute developmental noise increases with increasing size, although relative error declines somewhat, and that this component is relatively

A.



B.



C.

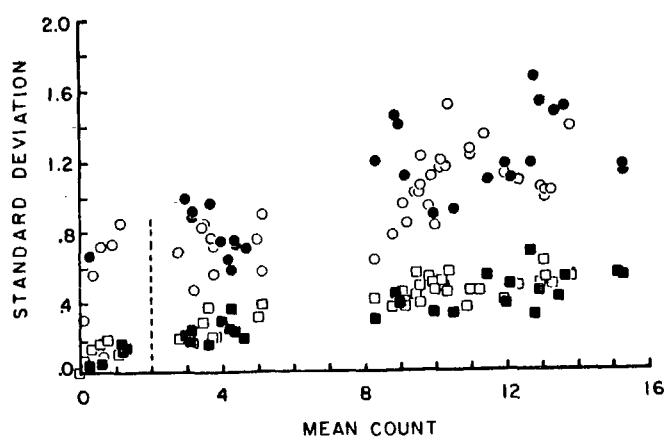


Fig. 7. Relationship between sample standard deviations and sample mean length or count. A. Mucrones (○) and antennules (●) compared with estimates of measurement error (connected dots). B. Mucrone sutures (below 7) and antennule segments (above 7). Samples from the three New England lakes (Occom Pond, Lake Mitchell, and Lake Norford) but expanded over the seasonal set. C. Between-individual (○, ●) and within-individual (□, ■, ANOVA estimate) components. Open and closed symbols represent counts by two independent investigators. Samples come from New England lake survey studies.

Table 3. Change in C.V. with increased magnification, a test of measurement error. Two samples measured under different magnifications, i.e. with increasing precision, to see if relative error declines. Source—Occum Pond, N.H.

Magnification	<i>N</i>	Mean*	SD	C.V.	±95% C.L.†
200	40	0.423	0.121	0.286	0.063
	40	0.405	0.111	0.274	0.060
320	40	0.660	0.195	0.295	0.065
	40	0.641	0.173	0.270	0.059
500‡	40	1.075	0.324	0.301	0.066
	40	1.080	0.266	0.246	0.054
800	40	1.630	0.420	0.257	0.056
	40	1.603	0.404	0.252	0.055

* Microscope units (scale reads to tenths; at 500×, 18.3 times units = microns).

† None of the coefficients of variation are significantly different from each other.

‡ Typical measurement magnification for mucro length.

minor compared to the contribution of between-individual variation. Inflation of the C.V. near the origin is largely attributable to the between-individual component, not to measurement error or to the within-individual component.

Variation of structural components relative to the whole—Although measurement error contributes some to the variance of small mucrones, real lower variability of an entire structure relative to its parts can arise from two principal properties: systematic decrease in the inherent variability of parts as the structure gets longer, or random variation in assembly of parts (either within or between individuals). In the first case, initial cells in a sequence are more variable in length than subsequent ones. As the number of uniform cells increases, $C.V._c$ (the C.V. component for cell length) will decline, as well as $C.V._s$ (the C.V. component for total spine length). In the second case, differences in the component lengths of highly variable units average out as the sum increases. For example, a mucro constructed of a short cell followed by a long cell will sum to the same total length as a mucro composed of a long cell followed by a short. For lower correlations between components, both within and between individuals, $C.V._c$ should remain similar, but $C.V._s$ for the sum will decline (Pearson-Davin effect: *see materials and methods*).

Detailed examination of component/

Table 4. Component/whole contrasts in coefficients of variation (sample from Third Sister Lake, Michigan). Coefficients of variation for component cell lengths ($C.V._c$) are contrasted with those for the entire spine length ($C.V._s$). Symbols follow sample equivalent parameters for Eq. 9. ($C.V._c$ —component cell length; $C.V._s$ —sum of cell lengths, also length of entire structure; r —correlation coefficient between component cell lengths; $C.V._{max}$ —maximum value expected, equal to weighted average of component coefficients of variation). Additional information on measurement error is included (measurements at $800\times$, recorded in ocular units).

Component/whole contrast															
A. One-cell individuals															
Side	N	\bar{x}	$C.V._c$												
Left	15	1.49	0.117												
Right	14	1.42	0.114												
B. Two-cell individuals															
Side	N	\bar{x}_1	$C.V._c$	\bar{x}_2	$C.V._c$	r_{ij}	P	Obs. $C.V._s$		Max $C.V._s$					
Left	23	1.20	0.327	0.70	0.206	0.354	0.09	0.249		0.282					
Right	26	1.16	0.275	0.86	0.246	0.228	0.27	0.219		0.264					
C. Three-cell individuals															
Side	N	\bar{x}_1	$C.V._c$	\bar{x}_2	$C.V._c$	\bar{x}_3	$C.V._c$	r_{12}	P	r_{13}	P	r_{23}	P	Obs. $C.V._s$	Max $C.V._s$
Left	21	0.87	0.318	0.71	0.228	0.78	0.197	-0.094	0.8	-0.279	0.2	0.669	0.001	0.074	0.273
Right	19	0.89	0.210	0.70	0.211	0.75	0.156	0.286	0.1	-0.057	0.8	0.087	0.7	0.056	0.193
Measurement error															
Part	\bar{x}		SD		$C.V._c$		Relative error ($C.V._c/C.V._s$)		% Variance						
Component	0.78		0.037		0.047		12.2		14.9						
Whole	2.36		0.045		0.019		7.0		6.7						

whole variation in samples reveals that both systematic differences in variability and statistical properties are contributing to observed trends. Shorter spines are more variable than longer ones, yet the correlations between components are also low (Table 4). These patterns are produced in part because, at short to intermediate spine lengths, many individuals that possess few cells have disproportionately elongated those cells. From the standpoint of ultimate fitness value, the total length of the spine is important, not whether it is composed of many small cells or fewer elongated ones. If the total lengths are equivalent, the construction details are relatively unimportant unless construction compromises integrity.

Two examples illustrate operation of the above two properties (Fig. 8). Here the component lengths are the distances between suture boundaries on mucrones, presumably indicating cell lengths that comprise the total length of the defensive spine. In the Third Sister Lake sample, notice that length variation in all the component parts is quite high, $C.V._c = 0.41$ for left cell lengths

and 0.36 for right, whereas it is lower in the Lake Norford sample. If the position of cells is numbered sequentially from 1 (basal cell) to 7, then the $C.V._s$ for successive sums along the mucrones can be compared with component values ($C.V._c$). In the Third Sister Lake sample, the decline is substantial from the initial basal value (0-1), to the sum of the lengths for the first two cells (0-2), to finally the sum of three cell lengths (0-3). $C.V._s$ declines from a component value of 0.36-0.28 to a final sum value of 0.11-0.10, mirroring the observed decline for seasonal and geographic samples (Fig. 8A). The total number of individuals in the sum totals also declines because fewer individuals possess higher cell counts. Comparison of component values in three-celled individuals shows that additional cells are more uniform, although component values never achieve the very low values of entire sums of either three-celled or six-celled individuals (Fig. 8B). Longer featured clones generally have more uniform mucrones, as shown in both samples. The component parts of mucrones are less variable in the Lake Norford sam-

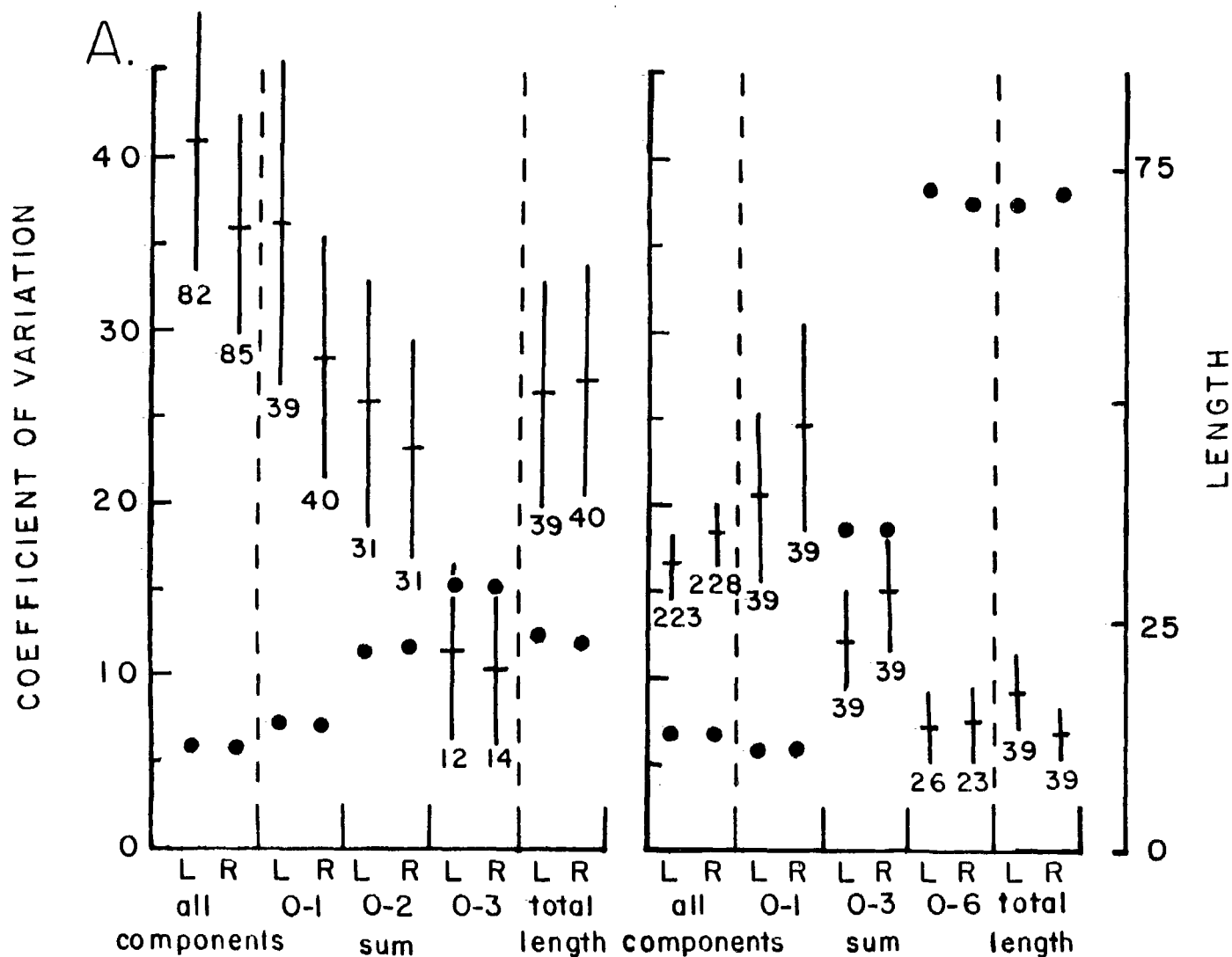


Fig. 8. Component/whole relationships of mucrones in two field samples (intermediates, Third Sister Lake, Michigan; long-featured, Lake Norford, Vermont) illustrating summation (C.V.) and component (C.V.) declines in coefficients of variation. A. Effects of summation on cell lengths. Note how C.V. declines as more cells are measured (horizontal and vertical lines indicate $V \pm 95\%$ C.L.; dots record absolute length of components, sums, or entire spines). B. Component C.V. for three-celled Third Sister Lake individuals and entire Lake Norford sample. Note how component C.V. declines progressively as more cells are added.

ple, yet again there is a significant decline due to summation and the central limit theorem.

In these samples, the systematic decrease in C.V. arises also because the additional cells in longer spines are more uniform in size. Basal cell lengths seem more highly variable in the intermediate-length sample. In this sample there is a noticeable inverse relationship between cell size and cell number, for the cell lengths of one-celled (1.45 units, $SD = 0.19$, $n = 17$) and two-celled mucrones (1.19 units, $SD = 0.41$, $n = 36$) are much longer than those of three-celled mucrones (0.94 units, $SD = 0.28$, $n = 26$). Certain individuals, and presumably clones, elongate their cells to approach more closely the total length of multicelled individuals. This compensation is also evident in left-

right side comparisons, e.g. if the left mucro contains fewer cells, those cells will be longer. Perhaps in *Bosmina* the original impetus for induction arose from such developmental compensations.

Discussion

The use of coefficients of variation to characterize morphological variation in zooplankton defensive spines revealed some strong, but initially puzzling, patterns. Selection for increased spine length in field populations (the rotifer *Brachionus*; the cladocerans *Bosmina* and *Daphnia*) produced significant declines in C.V. There was also remarkable similarity between cases, as coefficients of variation of small spines were initially near 30%, then declined to around 7-8%.

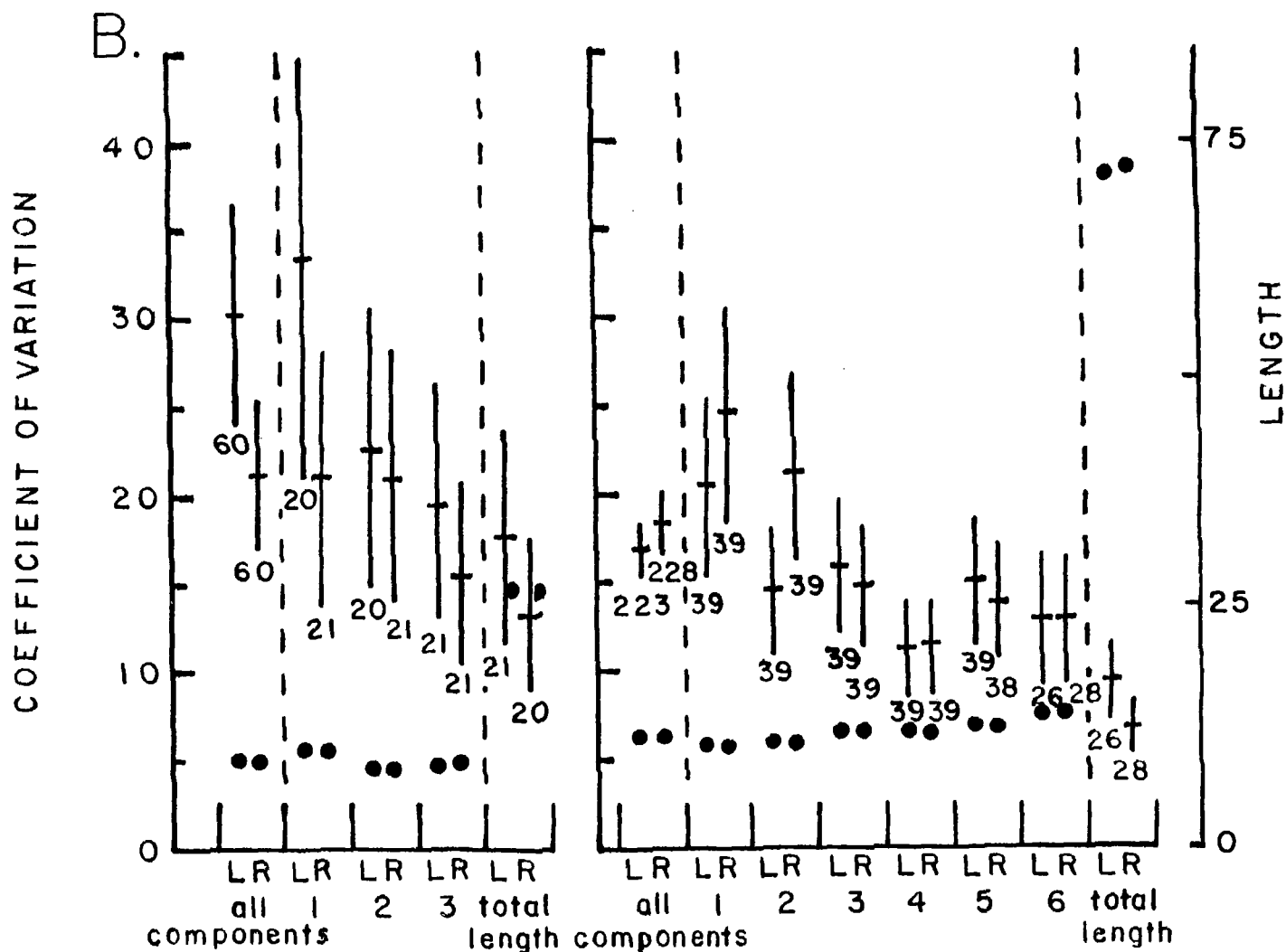


Fig. 8. Continued.

Detailed examination of *Bosmina* mucrones and antennules disclosed an almost hyperbolic inverse relationship between C.V. and mean spine length. The relationship was evident in selection experiments, seasonal and geographical survey data. Trends were similar for both length measurements and cell counts (sutures, segments), although polymorphism in antennules elevated coefficients of variation for small length measurements.

In *Bosmina*, the general trends seem attributable to a combination of two interesting biological and statistical properties. Although confidence limits around C.V., make discrimination between different models difficult, precise measurements demonstrate that small spines are inherently more variable than longer ones. Small

mucrones show greater proportional variation in size, shape, and internal cell pattern than their longer, functional counterparts. These small spines seem to be rudimentary structures, at least in many cases. Initial within-individual vs. between-individual comparisons suggest that the elevated C.V. values in small- to intermediate length mucrones are attributable to both developmental "noise" and between-clonal differences, with the latter contributing most of the variance.

There are alternative ways for development to achieve small to intermediate spine lengths. Certain clones lengthen mucrones and antennules by adding cells, while others elongate existing cells. Some even produce spikelike mucrones composed of elongated single or double cells (Kerfoot 1987). As

long as their component parts sum to the same length and the spines retain integrity, the degree of protection should be equivalent.

For short-featured forms, morphological variation probably has little influence on overall fitness. There is presumably little direct selection from predatory copepods, as clones adapted to low mortality coexist with regressed inducible clones. At intermediate spine lengths, natural selection permits moderate variation (alternative developmental pathways) because the internal construction of a spine is less important than its eventual length. Under intense selection, there is probably loss of genetic variance because so few clones can produce extremely long mucrones and antennules.

The alternative construction patterns of spines and the random variation of parts has repercussions on particular statistical properties. The sampling relationship between the standard deviation and mean differs in notable respects from that expected in a simple two-parameter lognormal distribution. Within-individual measures (bilateral asymmetry) show that absolute developmental "noise" increases with longer features, yet the increase in within-individual and between-individual measures is less than expected, i.e. it is not directly proportional to the absolute mean length.

The statistical basis of this pattern is general and probably applies to many morphometric characters. In *Bosmina*, the elements that make up the mucrones and antennules are more variable in length than their sum, i.e. the entire structure itself. If the sizes of the units that comprise larger structures are poorly correlated with each other (both within and between clones), then the longer the structure, the lower the expected C.V. If elements are truly random, which they are not, then the C.V. is expected to decline proportional to the square root of length or count (Pearson and Davin 1924; Lande 1977; Soule 1982). If there is some correlation, the initial decline is still marked, but longer structures show less decline in C.V. Attempts to fit linear regressions to observed data produce lower slopes than expected from mean C.V.s, with positive (artificial) intercepts on the y-axis (Fig. 3A).

This pattern is characteristic of most data sets and is attributed to a combination of real reduction in inherent variation and to a statistical property of large, random numbers known as the central limit theorem.

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