

Aggregation, Transformation, and the Design of Benthos Sampling Programs¹

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Solutions are offered to the problems of data transformation and the design of efficient programs for sampling the benthos of lakes and large rivers. All types of benthic animals from many types of substrate, sampled with diverse sampling gear, are aggregated in a similar fashion. Aggregation can be indexed by the unbiased exponent of the power relationship between density and variance. A single variance stabilizing transformation can be used for all macrobenthos population data since the relationship of sample variance to mean density is similar in all taxa of benthic animals. Stabilized variance in population data satisfies one of the main assumptions of the analysis of variance and allows use of normal statistics provided that the other assumptions are met. The fourth-root transformation stabilized the variance in all macrobenthos samples while either the commonly used square root or logarithmic transformations did not. Sampling programs can be optimized empirically. Standard deviation (s) is predictable from mean density (M ; m^{-2}) and sampler size (A ; cm^2) from the equation: $\log_{10}s = 0.581 + 0.696 \log_{10}M - 2.82 \times 10^{-4}A$. The data show that it is easier to obtain a precise estimate of macrobenthos density at high densities. Small diameter samplers are most efficient in obtaining high levels of precision. Data were taken from the literature.

Key words: aggregation, benthos, freshwater, regression, sampling, transformation

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L'auteur offre des solutions aux problèmes de transformation des données et conception de programmes efficaces d'échantillonnage du benthos de lacs et de grandes rivières. Tous les types d'animaux benthiques habitant divers types de substrats, échantillonnés à l'aide d'engins différents, sont groupés de la même façon. Un indice d'agrégation peut être déduit d'un exposant non biaisé de la relation géométrique entre densité et variance. On peut utiliser une seule variance stabilisant la transformation pour toutes les données sur les populations macrobenthiques, puisque la relation entre variance d'échantillonnage et densité moyenne est semblable dans tous les taxons d'animaux benthiques. La variance stabilisée dans les données sur les populations est conforme à l'une des principales hypothèses d'analyse de variance et permet l'emploi de statistiques normales, pourvu que l'on se conforme aux autres hypothèses. La transformation à la quatrième racine a pour effet de stabiliser la variance dans tous les échantillons de macrobenthos, alors que ce n'est pas le cas pour les transformations en racines carrées ou logarithmiques communément utilisées. On peut optimiser empiriquement les programmes d'échantillonnage. Il est possible de prédire l'écart type (s) à partir de la densité moyenne (M ; m^{-2}) et la taille de l'appareil d'échantillonnage (A ; cm^2) à partir de l'équation : $\log_{10}s = 0,581 + 0,696 \log_{10}M - 2,82 \times 10^{-4}A$. Les données démontrent qu'on obtient plus facilement une estimation de la densité du macrobenthos à de hautes densités. Des appareils d'échantillonnage de faible diamètre permettent d'atteindre de plus hauts niveaux de précision. Les données ont été extraites de travaux publiés.

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BENTHIC population estimates made in lakes and large rivers are highly variable. This is due to their distribution which is usually aggregated or contagious (Elliott 1977). Analysis of data and the design of sampling surveys for aggregated populations are difficult, yet are of great importance if we wish to make precise estimates

of benthic populations. The problems involved in making biomass estimates of benthic animals are even more difficult since precise estimates of both population and weight must be made. In this paper I offer solutions to the problems of aggregation, treatment of data, and the design of sampling surveys, towards the precise estimation of benthos population density.

Many measurements of the aggregation of organisms in space have been proposed (e.g. Elliott 1977; Southwood 1966; Paloheimo and Vukov 1976). Indices of aggregation fall into two categories: those

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that can be derived from population estimates from sets of randomly placed samples, and those that must be derived from measures of distance between individuals. Although indices based on the spacing of individuals are the best measures of aggregation (Paloheimo and Vukov 1976), these indices will not be discussed here because they are impossible to apply to small animals which cannot be observed directly. Only the indices calculable from distributions of population estimates such as those collected by grabs and corers will be considered here. In this paper I apply one of these indices to a large body of benthic data to examine the tendency of organisms to aggregate.

The amount of clumping that we find will dictate the method of data analysis. Since benthic population estimates are usually found to be contagious, the distribution of density estimates of any particular population will be nonnormal and nonrandom. Aggregated data require the use of nonparametric statistical techniques or data transformation prior to parametric statistical analysis. Easy-to-use nonparametric techniques (Conover 1971) should be used for hypothesis testing in situations where data cannot be made to conform to the assumptions of analysis of variance. In many cases, the use of statistical methods based on the normal distribution is more desirable because these methods are useful in summarizing the structure underlying a body of data (Andrews et al. 1971). I will discuss only the transformation of data toward the use of parametric statistics because parametric techniques are widely available and understood, are dominant in computer packages of statistical programs, and are simple to compute.

The second section of this article is a guide to the researcher in the design of sampling programs. The conclusions were derived from published benthic data. This paper suggests ways in which more interpretable data can be collected and ways of interpreting benthos data more precisely.

Data and Analysis

The data used in this analysis were collected from published literature as well as government reports. A survey

was made of the articles listed in *Biological Abstracts* for the years 1968–78 (Index: benthic, benthos, bottom, macrobenthos, sediment). Over 600 abstracts were screened in this manner from which 260 papers were examined. A computer literature survey done by the New England River Basins Commission (Key words: benthos, benthic, macrobenthos, and related terms) yielded 1126 abstracts and many sets of data. While many of the papers promised "quantitative" data, only 23 papers yielded data for the data set because many authors reported only mean densities and no measure of dispersion.

The data set derived from the literature consists of measures of mean density (\bar{x}) and variance (s^2) for various taxa and groups of taxa; also included are sampler type, sampler size, number of replicates, and sediment type. Nearly all of the data were counts of animals retained on a 500–600 μm mesh. Some samples (52 sets out of 1462) were obtained using a 270–350 μm mesh. These samples did not perform differently than those sieved with larger screens. Data from studies in which subsampling occurred were rare and were not included. The data are available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2. I also have a computer tape available for those wishing to perform further analysis.

The data set discussed here contains estimates of benthic populations and dispersion from many countries around the world. No data were rejected on grounds other than lack of true replication (i.e. replicates all taken same time, same station, same sampler). The data set was constructed primarily for examination of the freshwater benthos of lakes, ponds, and large rivers.

Regression analysis is used to fit linear functions to sets of data points throughout this paper. Although both variables were subject to error, linear regression analysis was performed using the Model I or least-squares method ($b = \Sigma xy / \Sigma x^2$). Model I regression was used instead of the computationally complex Model II (Sokal and Rohlf 1969) analysis because of the large amount of data processed. Model II regressions were also performed on subsets of the data using Bartlett's three-group method (Sokal and Rohlf 1969); slopes, intercepts, and confidence intervals of slopes were very similar to those found using Model I techniques (Table 1). The similarity of estimates by both techniques is due to large sample sizes and high correlations between variables (Ricker 1973).

TABLE 1. Comparison of Model I (least squares) and Model II (Bartlett's three group method — Sokal and Rohlf 1969) techniques for the estimation of slopes (b) and confidence intervals of slopes (95% C.I.) for log-log regressions of s^2 on the \bar{x} of replicate benthos samples. n indicates the number of sets of data used in the analysis and r^2 is the coefficient of determination (Steel and Torrie 1960). The data indicate that there is little difference between the results of the two methods of estimation.

Taxon	n	r^2	Model I		Model II	
			b	95% C.I.	b	95% C.I.
Acari	22	0.98	1.71	1.59–1.83	1.68	1.52–1.83
Hirudinae	34	0.54	1.04	0.70–1.39	1.03	0.59–1.46
Nematoda	24	0.88	1.78	1.49–2.07	1.66	1.37–1.86
Platyhelminthes	34	0.87	1.56	1.34–1.77	1.43	1.14–1.68

Aggregation and Transformation

AGGREGATION

Not only is the aggregation of organisms of interest to ecologists from a behavioral standpoint, but to analyze population data properly it is also necessary to measure the degree of aggregation accurately. Many measures of aggregation have been derived but few are useful since most vary with factors other than the aggregation of the animals. Among the most popular indices of aggregation have been the variants of variance (s^2) to mean (\bar{x}) ratio (Elliott 1977). Some examples are:

$$\frac{s^2}{\bar{x}}, \frac{s^2(n-1)}{\bar{x}}, \frac{s^2}{\bar{x}-1}, \frac{s}{\bar{x}}, \frac{100\sqrt{s^2-\bar{x}}}{\bar{x}}, \frac{(s^2/\bar{x})-1}{\Sigma X-1}$$

where s is the standard deviation, n the number of samples, and ΣX the sum of all animals in a set of replicate samples. The $s^2:\bar{x}$ indices are difficult to apply among sites or dates since apparent aggregation will vary with the mean density even if the variance remains constant. This aspect of the variance to mean ratio might lead to equivalent measures of aggregation if differences in s^2 and \bar{x} , between sites or dates, balance each other (Elliott 1977).

Another commonly used index which is also sensitive to variation in \bar{x} is k of the negative binomial distribution ($s^2 = \bar{x} + \bar{x}^2/k$). Morisita's index of contagion (1959; Southwood 1966) is not sensitive to variation in \bar{x} but is susceptible to variation in the area covered by the sampler. It usually cannot be used to compare aggregation between studies.

An index of contagion which can be used to compare aggregation among studies is the exponent in Taylor's Power Law (Taylor 1961). This measure of aggregation incorporates the density dependence of aggregative behavior and is thus free of the confounding effects of density (Taylor et al. 1978). Taylor's Power Function holds well over a range of sampler sizes (Paloheimo and Vukov 1976; Taylor and Taylor 1977), and can be calculated from literature values if some measure of dispersal is given with population data. Another advantage of the power function is that it can describe many types of distributions in one mathematical expression (Taylor 1965; Taylor et al. 1978). The index is calculated as the slope of the relationship between $\log s^2$ and $\log \bar{x}$, the exponent b in the expression:

$$(1) \quad s^2 = a\bar{x}^b$$

where \bar{x} is the arithmetic mean density and s^2 is the variance of a group of replicate samples. The constant a is a sampling factor (Southwood 1966). The exponent b can vary from negative to positive infinity and can describe a variety of distributions (Taylor 1965). Large values of b indicate increasing aggregation; $b > 1$ indicates a contagious distribution. Uniform or equally spaced distributions have $b < 1$. The special case of the random or Poisson distribution ($s^2 = \bar{x}$) occurs when $a = b = 1$.

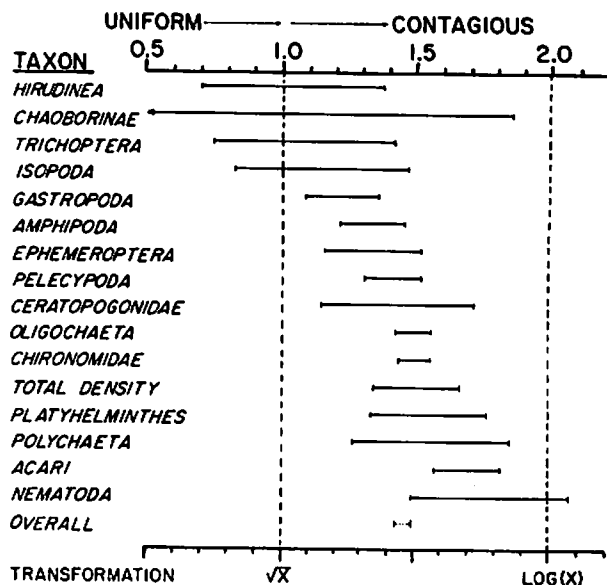


FIG. 1. The degree of contagion in groups of benthic animals shown as 95% confidence intervals of b from equation 1. Values of $b < 1$ indicate that animals are evenly spaced; values of $b > 1$ indicate that animals are aggregated. Transformations shown at the bottom are those values of b under which common transformations would be used (eq. 2).

The measure of aggregation, b , was calculated by simple linear regression analysis for many sets of data. The literature data were sorted and regressed to test the hypothesis that the degree of aggregation is constant among taxonomic groups, among sediment types, and among animals sampled with various sampling gear (Table 2).

Benthic animals in lakes and large rivers are aggregated. All power regressions of variance on the mean show significant positive relationships (Table 2). Most regressions of s^2 on the \bar{x} for group of animals have b significantly greater than 1. Few groups show significantly more or less aggregation than the others (see comparison of b in Fig. 1). Not even the least aggregated animals (lowest b), Hirudineae, Chaoborinae, Trichoptera, or Isopoda are randomly distributed ($a = b = 1$) because even though the confidence intervals of b overlaps one, a is greater than one (Table 2). Further, the variance was less than or equal to the mean in only 2.5% of 1500 sets of data examined. This indicates that the Poisson distribution is not a good model to describe the variability of benthos populations.

The degree of aggregation of animals in various sediment types is very similar as well (Fig. 2). Although all sediments hold animals aggregated to approximately the same extent, there is some tendency for animals to be less clumped in clays and more clumped in gravel (Fig. 2).

The type of sampler used also has little effect on the contagion of the benthos. The Smith-McIntyre grab

TABLE 2. Regression variables for power function regressions of variance (s^2) on mean density (M , m^{-2}) of benthos population estimates where $s^2 = a\bar{x}^b$, n is the number of sets of observations, r^2 is the coefficient of determination, and $1 - b/2$ is the exact variance stabilizing exponent (eq. 2). Chi square tests (Tsutakawa and Hewett 1977) were used to determine whether the regression lines are significantly different from the overall regression of $\log s^2$ on $\log \bar{x}$. Significant values of χ^2 indicate that the regression line shows a higher (+) or lower (-) variance overall. Asterisks indicate that test statistics are significant at $P < 0.01$ (**) or $P < 0.05$ (*), ns = not significant.

Data set	n	r^2	a	b	$1 - b/2$	χ^2 test
<i>Groups of animals</i>						
Acari	22	0.98**	3.03	1.708	0.15	ns
Amphipoda	92	0.84**	10.45	1.339	0.33	ns
Ceratopogonidae	5	0.99**	6.47	1.434	0.28	ns
Chaoborinae	4	0.94**	31.19	1.043	0.48	ns
Chironomidae	387	0.85**	3.94	1.498	0.25	ns
Ephremeroptera	47	0.83**	7.57	1.339	0.33	ns
Gastropoda	128	0.71**	11.48	1.223	0.39	ns
Hirudinae	34	0.54**	18.58	1.041	0.48	ns
Isopoda	10	0.89**	20.46	1.149	0.43	ns
Nematoda	24	0.88**	0.61	1.781	0.11	ns
Oligochaeta	286	0.86**	4.92	1.496	0.25	ns
Pelecypoda	138	0.83**	7.87	1.496	0.29	*(+)
Platyhelminthes	34	0.87**	4.18	1.557	0.22	ns
Polychaeta	13	0.92**	3.24	1.561	0.22	ns
Trichoptera	29	0.63**	13.21	1.084	0.46	ns
Total number	154	0.69**	3.10	1.512	0.24	**(-)
<i>Type of sediment</i>						
Clay, mud, gravel	29	0.78**	8.30	1.223	0.39	ns
Mud and detritus	31	0.84**	5.35	1.253	0.37	**(-)
Clay and sand	81	0.82**	8.22	1.259	0.37	ns
Clay and silt	58	0.63**	17.18	1.336	0.33	ns
Sand and mud	175	0.79**	7.59	1.340	0.33	ns
Sand and silt	106	0.75**	9.75	1.358	0.32	ns
Sand	95	0.85**	6.81	1.369	0.32	ns
Silt	121	0.88**	6.04	1.840	0.31	ns
Fluid mud	8	0.60*	24.21	1.411	0.29	ns
<i>Sagittaria</i>	12	0.74**	8.73	1.418	0.29	ns
Mud and gravel	30	0.70**	5.09	1.423	0.29	ns
Sand and gravel	71	0.87**	6.27	1.461	0.27	ns
Gravel	110	0.84**	5.04	1.468	0.27	ns
Mud	466	0.89**	5.16	1.495	0.25	ns
Fine sand	34	0.85**	1.68	1.687	0.16	ns
<i>Type of sampler</i>						
Allen Sampler	10	0.97**	16.00	1.323	0.34	*(+)
Ekman Grab	301	0.79**	18.97	1.247	0.38	ns
K-B Corer	37	0.87**	6.82	1.574	0.21	**(+)
Marukawa	10	0.74**	115.08	1.404	0.30	**(+)
Multiple Corer	4	0.99**	16.48	1.368	0.32	ns
Modified Ekman	7	0.97**	4.44	1.595	0.20	ns
Maitland Corer	4	0.99**	17.54	1.527	0.24	ns
Pearson Airlift	34	0.94**	12.25	1.467	0.27	**(+)
Petersen Grab	722	0.82**	6.43	1.343	0.33	ns
Ponar Grab	266	0.81**	7.31	1.399	0.30	*(-)
Smith-McIntyre	20	0.89**	1.29	1.764	0.12	ns
Surber	18	0.93**	5.00	1.531	0.23	ns
Overall	1462	0.87**	5.24	1.462	0.27	

gives rise to the highest b (most aggregation), possibly due to the intermittent loss of some surface sediments from pressure wave effects (Fig. 3).

In all cases differences in exponents are small. The

greatest variation in b is seen when data are regressed within taxa (Fig. 1-3). Tests of the hypothesis that groups of data vary from the overall regression of $\log s^2$: $\log \bar{x}$ show that few sets of data lie significantly above

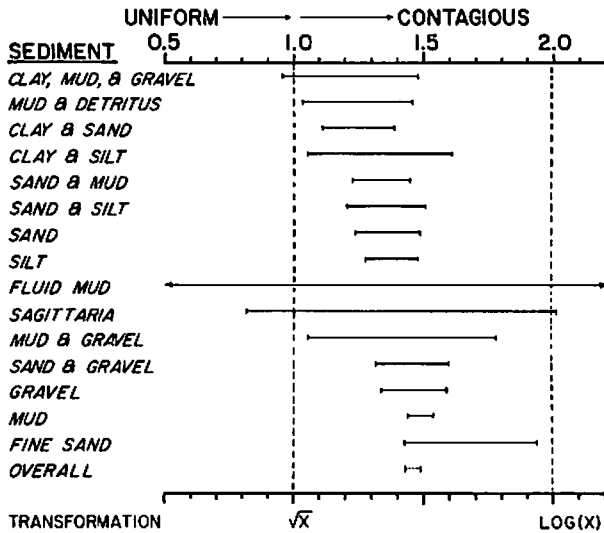


FIG. 2. The degree of contagion of benthic animals in various substrates shown as the 95% confidence intervals of b from equation 1. Values of $b < 1$ indicate that animals are evenly spaced; values of $b > 1$ indicate that animals are aggregated. Values of b under which common transformations would be used are shown at the bottom of the figure (eq. 2).

or below the overall $s^2:\bar{x}$ regression (Table 2) (nonparametric technique of Tsutakawa and Hewett 1977). The tests show that pelecypods yield a variance which is higher than expected for any given density and that counts of total benthos populations and populations collected from mixtures of mud and detritus yield a vari-

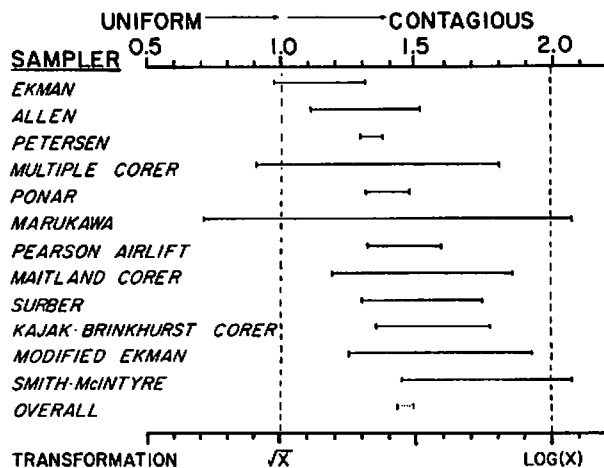


FIG. 3. The degree of contagion of benthic animals taken with various sampling gear shown as the 95% confidence intervals of b from equation 1. Values of $b < 1$ indicate that animals are evenly spaced; values of $b > 1$ indicate that animals are aggregated. Values of b under which common transformations would be used are shown at the bottom of the figure (eq. 2).

ance which is lower than expected for any density. When regression lines are calculated on data grouped by sampler there are significant differences among these regressions in spite of fairly uniform slopes (Fig. 3). These differences among regressions are probably due to elevation (increased a) which indicates that a is indeed a factor related to sampling conditions (Southwood 1966). The amount of aggregation (b), though, is roughly the same over all types of animals, sediments, and samplers.

The similarity of aggregation among groups of pooled data is not the result of broad confidence intervals due to failure to account for differences in aggregation (b) among sampling sites or investigators. If different systems or investigators gave rise to data aggregated in different ways, then pooled data would be made up of many different $s^2:\bar{x}$ relationships. A test of the homogeneity of data within a pooled regression should give us more confidence that we are not merely generating broad regressions which cannot be separated due to their heterogeneity. Mori (1976) studied the benthos of Lake Biwa (Japan) during 1972 and presented tables of raw data. Log-log regressions of variance and mean for homogeneous data (oligochaetes within sampling stations) were not different from the overall regression of $\log s^2$ on $\log \bar{x}$ (chi square tests, $P \geq 0.01$). The similarity of the most homogeneous data with the over-all regression was an example chosen at random which indicates the homogeneity of $s^2:\bar{x}$ data. Log-log regressions of s^2 on \bar{x} for oligochaetes within stations had r^2 values: 0.01 at station Ie-1; 0.39 at station Nb-2; 0.03 at station Nb-5; and 0.60 at station Na-3. These r^2 values are all lower than the r^2 of 0.86 from pooled oligochaete data (range of \bar{x} within stations approximately equal to that overall). This example indicates that the maximum probability of separating slopes of $\log s^2:\log \bar{x}$ relationships (b), and thus separating differences in contagion, would be found in pooled calculations. The similarity of contagion among taxa, sediments, and samplers is real and reflects the basic similarity of the distribution of most types of benthos.

TRANSFORMATION

In order that parametric statistical methods may be applied to benthic data, the assumptions of normal analysis of variance must be satisfied. Some of the major assumptions of the analysis of variance are that the data are normally distributed, the errors are equal and uncorrelated with the magnitude of the means, and that the variance components are additive (see Scheefé 1959 for a thorough review). The seriousness of violating these assumptions will vary with the sort of hypothesis to be tested and the nature of the data. Scheefé (1959) found that if the number of samples is very large and constant among treatments, and both the skewness and kurtosis are constant among samples, then differences among means may be tested safely using parametric techniques without transformation to stabilize the vari-

ance. These conditions are rarely met in benthos studies since the number of samples obtainable at each station is often limited and the shapes of benthos density distributions vary widely. The consequences of this sort of violation of the assumptions of the analysis of variance can be severe and can cause invalid statistical inference (Scheefé 1959).

In many cases transformation will cause data to meet the assumptions of parametric analysis adequately. Many authors feel that transformation to stabilize the variance (remove correlation between the variance and the mean) will help to alleviate skewness in the distribution and increase the probability of additivity (Bliss and Owen 1958; Snedecor and Cochran 1967; Southwood 1966; Tukey 1968). Many types of analysis can be made more valid through transformation to stabilize the variance. These include: those analyses employing *F*- or *t*-tests (Aveson and Schmitz 1970; Snedecor and Cochran 1967), linear regression (Hocking 1976), and the randomized complete block design (Lindsey 1976). In some cases, transformation to stabilize the variance will not be adequate and the conformity of the data to the assumptions of the analysis of variance should be tested (Scheefé 1959).

Taylor (1961) showed that an exact variance stabilizing function (transformation) can be calculated if the power relationship of the variance to the mean (eq. 1) is known. This paper (Table 2; Fig. 1, 2, 3) and many others (see Southwood 1966 for review) demonstrate that in ecological data the variance often increases with the mean ($b > 0$). Taylor (1961) found that this relationship obeys a power law and that the variance in groups of population estimates can be stabilized by transforming the original data:

$$(2) \quad X' = X^{1-b/2}$$

where X is an individual population estimate (number of animals in single grab sample or number m^{-2}), X' the transformed datum, and b is the exponent found in equation 1. If b is 1 then the square root transformation

is used, if b is 2 then the log transformation has been recommended (Taylor 1965). For all other situations exact transformations can be calculated. Normal statistical methods are performed using the transformed data.

Because the slope of the log-log regressions of variance and mean of benthic population estimates are all approximately the same (Fig. 1-3), a transformation suitable for all benthic data can be derived. Exact transformations for specific types of data are listed in Table 2. Few exact power transformations are significantly different from the others regardless of type of animal, sediment, or sampling gear used. Exact transformations for benthic data seldom overlap the square-root transformation ($b = 1$, $1 - b/2 = 0.5$) or the log transformation ($b = 2$, $1 - b/2 = 0$) which are the common transformations recommended for the transformation of benthic population estimates (Elliott 1977). A universal transformation calculated from the overall regression of s^2 and \bar{x} (Table 2), is not significantly different from the fourth-root transformation. That is:

$$(3) \quad X' = X^{0.25}$$

This transformation can be applied successfully to most benthic data.

The utility of the fourth root transformation in the analysis of benthic data is illustrated in Table 3. If the transformation is adequate then transformed data should show no relationship between the variance and the mean. Table 3 shows r^2 values for log-log regressions between the variance and the mean of untransformed and transformed data. All untransformed data show significant relationships between variance and mean; loss of the significant relationship after transformation indicates that the variance was stabilized by the transformation. The fourth-root transform always stabilized the variance while the square-root and log transformations recommended by Elliott (1977) failed in some cases. In cases where the r^2 after fourth-root transformation is large but not statistically significant, more stability could be gained by attention to the exact size

TABLE 3. Coefficients of determination (r^2) of relationship between $\log_{10}s^2$ and $\log_{10}\bar{x}$ for untransformed data and data transformed with the square root ($x^{0.5}$), fourth root ($x^{0.25}$), and logarithmic ($\ln[x+1]$) transformations. * indicates that there is a significant ($P < 0.05$) correlation between s^2 and \bar{x} . Only samples with greater than three organisms per sampler were included because s^2 cannot be stabilized if $\bar{x} \leq 3$ (Andersen 1965).

Author/Station	n	r^2				b
		Untransformed	$x^{0.5}$	$x^{0.25}$	$\ln(x+1)$	
Hiltunen (1971)/#1	14	0.68*	0.05	0.18	0.26	1.34
Hiltunen (1971)/#1	7	0.76*	0.07	0.23	0.72*	1.18
Hiltunen (1971)/#4	12	0.67*	0.05	0.17	0.07	1.60
Koss et al. (1974)/1G	7	0.73*	0.34	0.09	0.01	2.28
Mori (1976)/Nb-2	10	0.72*	0.17	0.007	0.01	1.80
Mori (1976)/Na-3 (Jan.-Dec.)	18	0.61*	0.22*	0.04	0.001	2.04
Mori (1976)/Na-3	6	0.97*	0.86*	0.60	0.34	2.36

TABLE 4. Analysis of variance table for regression of $\log_{10}s$ predicted by $\log_{10}M$ ($\bar{x} \cdot m^{-2}$) and area covered by sampler (eq. 4). F' (partial F value) is calculated as the increase in Model SS when the variable in question is entered into the multiple regression as the last variable. F' is a measure of the variation in $\log_{10}s$ accounted for by each independent variable. The probability of gaining any of these F and F' values by chance is $\ll 0.0001$.

Source of variation	df	SS	F	r^2
Model ($\log_{10}s = \log_{10}M + \text{Area}$)	2	718	5285	0.88
Error	1433	97		
Total	1435	816		
Independent variable	F'			
$\log_{10}M$	7456			
Area	84			

of b in equation 2, rather than using the universal approximation of $b = 1.5$ ($1 - b/2 = 0.25$). If b , calculated for the specific set of data, is significantly different from 1.5, the exact transformation should be used and not the universal one (eq. 3). This will lead to more frequent satisfaction of the assumptions of parametric analysis.

Design of Sampling Programs

The primary concern in designing a sampling scheme is to gain an accurate measurement with high precision for the least effort. The size of the sampler or quadrat, and the number of replicate samples taken can be varied so that the minimum number of samples of minimum size may be extracted to yield a specified degree of precision. To date, the only means of calculating the number of samples needed to yield a certain precision has been to make some assumptions about the distribution of data and the relationship of the variance to the mean (Elliott 1977). Knowing the relationship of sample variance to density, sampler size, and number of sam-

ples taken would permit precise estimation of sampling requirements (Cochran 1977).

I have shown that the variance of a set of replicates is predictable from the mean density alone with a high degree of precision (Table 2). Using multiple regression analysis, I have found that the standard deviation (s) is predictable from the mean density, and that a significant amount of residual variation in the standard deviation is accounted for by sampler size (Table 4). The regression equation ($r^2 = 0.88$) to predict the standard deviation (s) is:

$$(4) \quad \log_{10}s = 0.581 + 0.696 \log_{10}M - 2.82 \times 10^{-4}A$$

where M is the mean density in numbers m^{-2} and A is the area of the sampler in cm^2 . The equation will provide unbiased predictions of $\log_{10}s$ in spite of the fact that M is measured with error, provided that M is measured under the same experimental conditions as those that were used to produce the regression equation (Guest 1961). This regression holds within the range of M of 3.0–48 000, the range of A of 15.2–2500, and the number of replicates from 2 to 54.

The precision of predictions made with equation 4 is shown as a comparison of observed and predicted values in Table 5. The observations in Table 5 were not used in the sampling survey from which the regression was derived, nor were any data from that lake or data collected with that sampler included. Observed and predicted standard deviations are quite similar. Predictions deviate from observations by 5 to 50% of the observed standard deviation.

Equation 4 can be used to predict s for proposed sampling surveys. The input variables are only the size of available sampling gear and the mean density of animals to be encountered. A guide to the distribution of densities of taxa and groups of taxa (Fig. 4) can be used to guess at the densities which will be encountered in the field.

Because the standard error (SE) is s/\sqrt{n} , and SE/\bar{x}

TABLE 5. Comparison of observed and predicted standard deviation(s) for data from Krezoski et al. (1978). Predicted values of s are from equation 4. Columns labelled \hat{s} are values of s predicted using the Poisson or negative binomial models (Elliott 1977).

Sample: Sample	Number m^{-2}	Observed s	Predicted s (this paper)	\hat{s} :Poisson	\hat{s} : $k=2$
Station 14					
Amphipoda	2912	1015	959	54	2059
Diptera	48	111	55	7	35
Oligochaeta	5661	2099	1524	75	4003
Pelecypoda	471	371	270	22	334
Total number	9092	2470	2120	95	6429
Station 18					
Amphipoda	2678	838	904	52	1894
Mysidacea	48	111	55	7	35
Oligochaeta	634	617	333	25	449
Pelecypoda	705	530	356	27	499
Total number	4065	1053	1209	64	2875

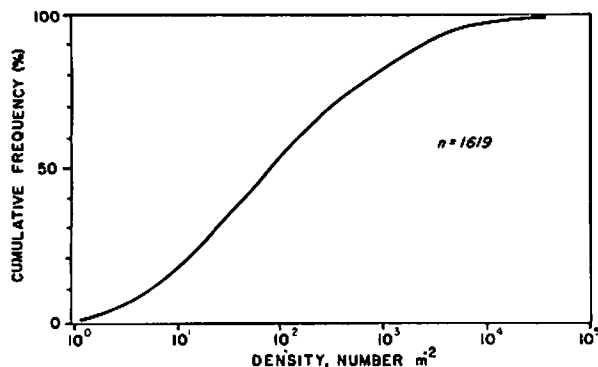


FIG. 4. Cumulative percent frequency of macrobenthos found in literature survey. This figure should be read "Y% of benthos densities are less than X m⁻²."

is a good measure of precision, we can use equation 4 to optimize sampling programs. The most probable SE can be calculated:

$$(5) \quad SE = \frac{(\text{antilog}(0.581 + 0.696 \log M - 2.82 \times 10^{-4}A))}{\sqrt{n}}$$

where *n* is the number of replicate samples. Rearranging equation 5 slightly and substituting the acceptable level of precision (*P*) in terms of *M* in place of the SE:

$$(6) \quad n = \frac{((\text{antilog}(0.581 + 0.696 \log M - 2.82 \times 10^{-4}A)) / PM)^2}{}$$

For example, if the desired level of precision is SE equal to 20% of the mean density, then *P* = 0.2. Solving equation 6 will tell us the most probable number of samples of any size we must take to gain the precision *P* at any density of animals. It should be noted that the confidence region around a predicted *s* will not be symmetrical due to the log transform in equation 4.

Because equations are difficult to evaluate, some example calculations of the number of samples necessary to obtain a precision of SE/ \bar{x} = 0.2 for various sampler sizes and densities are provided in Table 6. These calculations show that more samples must be taken with

small samplers and more samples must be taken at low density in order to obtain the same level of precision.

The objective in optimizing sampling programs is to gain the best precision for the least effort. In most benthic studies much of the effort is expended in processing the sediment (e.g. sieving, washing, counting). Optimization usually requires processing the least sediment for the greatest precision. The amount of sediment processed for a SE of 20% of the density can be found by multiplying the figures in Table 6 by the area of the sampler. The smaller numbers in Table 7 show which regime is the most profitable. Where processing sediment makes up the greatest portion of the sampling labor, the amount of work necessary to gain any level of precision decreases as the density of the population under study increases. The amount of work necessary increases with the size of the sampling device. Where sampling itself is difficult, subsampling of large samples might be considered. Statistical inference would only be valid to the large sample, if subsampling is used.

Looking back to Fig. 4 and Table 6 it is obvious why many benthic population estimates seem variable. In studies with replicate estimates the most frequent number of samples taken was 3. In such studies a SE equal to 20% of the mean density would be found consistently only at density greater than 1000 animals m⁻². Less than 20% of the densities of benthos found in nature lie above 1000 animals m⁻² (Fig. 4) and thus 80% of the SE's found taking three replicates will be greater than 20% of the mean. This situation could easily be remedied by taking many samples with a small sampler, thus increasing precision without much increase in effort (Table 7).

The technique presented here for planning sampling surveys differs from that of Elliott (1977) in that no assumptions are made regarding the distribution of benthic animals in nature. Elliott's technique requires the adoption of an algorithm for calculating the variance (*s*²), then dividing *s* by \sqrt{n} to calculate the expected SE. The formula for *s*² depends upon the assumed distribution which is either measured once or simply guessed and assumed to remain constant. Elliott (1977) sug-

TABLE 6. Number of replicate samples needed for various sampler sizes and macrobenthos densities in order that the SE of replicate samples average 20% of the mean density. Calculations are from eq. 6.

Density number m ⁻²	Size of sampler (cm ²)						
	20	50	100	250	500	750	1000
30	32	31	30	24	17	13	9
50	24	23	21	18	13	9	7
100	16	15	14	12	8	6	4
300	8	8	7	6	4	3	2
500	6	6	5	4	3	2	2
1000	4	4	3	3	2	<2	<2
5000	<2	<2	<2	<2	<2	<2	<2
10 000	<2	<2	<2	<2	<2	<2	<2

See
Errata

TABLE 7. Area of sediment (cm^2) that must be sampled, sieved, and sorted in order that the SE of replicate samples average 20% of the mean density, for various sampler sizes and macrobenthos densities. Figures are number of samples (Table 5) multiplied by the area of the sampler used. Calculations are from Table 5.

Density number m^{-2}	Size of sampler (cm^2)						
	20	50	100	250	500	750	1000
30	640	1550	3000	6000	8500	9750	9000
50	480	1150	2100	4500	6500	6750	7000
100	320	750	1400	3000	4000	4500	4000
300	160	400	700	1500	2000	2250	2000
500	120	300	500	1000	1500	1500	2000
1000	80	200	300	750	1000	1500	2000
5000	40	100	200	500	1000	1500	2000
10 000	40	100	200	500	1000	1500	2000

See
Errata

gests that the Poisson distribution where $s^2 = \bar{x}$ or the negative binomial distribution ($k = 2$) where $s^2 = \bar{x} + (\bar{x}^2)/k$ provide good approximations of the variability of benthos samples. The equation which I present for calculating s (eq. 4) is empirically derived from published data. The advantages of the empirical technique can be seen when compared to the results assuming the Poisson or negative binomial with constant k (Table 5). If the Poisson is assumed when planning a sampling survey, then s will be underestimated and too few samples will be taken. If the negative binomial is assumed, then in some cases s will be greatly overestimated and too many samples will be taken.

The findings of this study will hold provided that future experimental techniques are similar to those which were included in the data set used here. For example, care should be taken to use a sampling technique suited to the substrate (Kajak 1971) so that no extra variability is introduced through improper sampling. All substrates are not represented in all sampler classes (Table 2) so this is an important consideration.

Though the data set is adequate for this analysis, I am constantly adding data for the testing of further hypotheses. Any quantitative data that readers have available would be welcomed.

SAMPLING THE STREAM BENTHOS

Recently a paper was published by Resh (1979) in which the stream benthos data of Needham and Usinger (1956) and Chutter and Noble (1966) were examined to find the number of samples required to gain a specified precision at various benthos densities. Resh found that the number of samples necessary to gain a specified precision increased with decreasing density. This result is similar to that shown in my Table 6 so I have compared one set of these streams benthos data with eq. 4 which was derived from the benthos of lakes and large rivers (Fig. 5). The predictions from eq. 4 are significantly lower than the variability seen by Chutter and Noble (1966) (Fig. 5) as well as the variability

seen by Needham and Usinger (1956). This suggests that the benthic animals of stream riffles are more variable than those of lakes and rivers, and that sampling programs for stream benthos should be constructed accordingly.

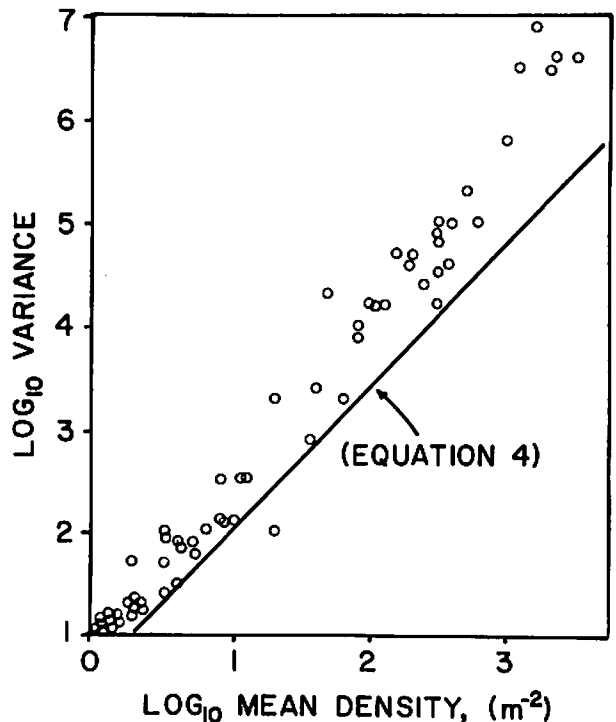


FIG. 5. The relationship of the variance to the mean in stream benthos samples compared to the relationship predicted by eq. 4. The stream benthos data are taken from Chutter and Noble (1966); each data point represents the mean and variance of a taxon (10 samples each). The least-squares regression equation to describe s^2 is: $s^2 = 7.24\bar{x}^{1.01}$ ($n = 69$; $r^2 = 0.97$). The figure shows that the benthos of lakes and large rivers are somewhat less variable than the benthos of a stream riffle.

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ERRATA

VOLUME 36, No. 12 — paper by J. A. Downing: *Aggregation, transformation, and the design of benthos sampling programs.*

PAGE 1461: equation 6 should be

$$(6) n = ((\text{antilog } (0.581 + 0.696 \log M - 2.82 \times 10^{-4}A))/PM)^2$$

and Table 6 should be

Density number m ⁻²	Size of sampler (cm ²)						
	20	50	100	250	500	750	1000
30	45	43	40	33	24	17	12
50	33	32	30	24	18	13	9
100	22	21	19	16	12	8	6
300	11	11	10	8	6	4	3
500	8	8	7	6	4	3	2
1000	5	5	5	4	3	2	<2
5000	<2	<2	<2	<2	<2	<2	<2
10 000	<2	<2	<2	<2	<2	<2	<2

PAGE 1462: Table 7 should be

Density number m ⁻²	Size of sampler (cm ²)						
	20	50	100	250	500	750	1000
30	900	2150	4000	8250	12 000	12 750	12 000
50	660	1600	3000	6000	9000	9750	9000
100	440	1050	1900	4000	6000	6000	6000
300	220	550	1000	2000	3000	3000	3000
500	160	400	700	1500	2000	2250	2000
1000	100	250	500	1000	1500	1500	2000
5000	40	100	200	500	1000	1500	2000
10 000	40	100	200	500	1000	1500	2000

Also see commentary in: *Can. J. Fish. Aquat. Sci.* 37: 1328-1332.