LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment on “Aggregation, Transformations, and the Design of Benthos Sampling Programs”

A recent article Aggregation, Transformations, and the Design of Benthos Sampling Programs by J. A. Downing (1979) reaches some conclusions which are, in my opinion, poorly supported by the data and analyses presented.

The major topic covered in this article was the possibility that aggregation in samples of benthic animals is constant, justifying a universal transformation to normalize benthic sampling data and providing a reliable way of predicting variances from means. To explore this possibility, the Taylor Power Law (Taylor 1961) was applied to a large number of data sets. This empirical relationship holds that for a population, the logarithm of variance is linearly related to the logarithm of the mean. The slope of this relationship, b, is used as a measure of aggregation. The approach proposed in the article is as follows:

The measure of aggregation, b, was calculated by simple linear regression for many sets of data. The literature 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...

Unfortunately, this interesting hypothesis is not tested in the article. There is no test of homogeneity of the b's. A common regression was calculated, and the non-parametric test of Tsutakawa and Hewett (1977) was used to compare subsets of the data composed of samples, of the same taxon or from the same sediment type or sampler (table 2). This test calculates the probability that the observed number of points from a subgroup lie above or below the common regression line. It is not a test of the slopes. This is obvious from table 2; among the taxa, Acari (b = 1.708, n = 22) and Hirudinea (b = 1.041, n = 34) are not significantly different from the common regression (b = 1.462) while Poreicypoda (b = 1.496, n = 138) is.

Although the question of heterogeneity is not answered explicitly, it is clear from fig. 1, 2 and 3 that there is significant heterogeneity among b's within all three classifications.

Despite these differences among b's, the conclusion is ultimately reached that “The amount of aggregation (b), though, is roughly the same over all types of animals, sediments, and samplers.” The author later states, “I have shown that the variance of a set of replicates is predictable from the mean density with a high degree of precision (table 2).” These statements are subjective appraisals of the results summarized in table 2 and not amenable to refutation. But the reader may rightly question what degrees of aggregation are “roughly the same.” The lowest b's in table 2 are about 1 (1.041, Hirudinea; 1.084, Trichoptera). A value of b = 1 is consistent with a random distribution of animals, although the intercept (a) should also be equal to 1, and this is not the case. However, the author does tell us that variance was less than, or equal to, the mean in 2.5% of the data sets examined. Therefore, we may conclude that benthic animals are sometimes randomly distributed, and examples of a = b = 1 may be found. It is also certain that uniform distributions exist (McLaughlin 1977). Their apparent rarity seems to reflect the distance between “replicates” in benthic work and the variable efficiency of samplers.

At the other extreme, the highest values of b in table 2 are about 1.8 (1.708, Acari; 1.840, silt samples; 1.764, Smith–McIntyre grab). A relevant question is the upper limit to b. It is often suggested that b = 2 indicates a log-normal distribution. I applied regressions of log s' on log x to negative binomial distributions over the range x = 1 to 125, and although the relationships are not linear, they approach linearity and b approaches 2 as k approaches 0. So the log series distribution presumably has b = 2. Also, another aggregated distribution is the two-phase mosaic. For sets of replicates where half the samples have no animals and the rest have some equal number, b = 2. Finally, for the extreme, suppose that sets of replicates all only had animals in one of the set, while the rest were empty. Again, b = 2, which reflects that so (x) is proportional to x, as if replicates were generated as multiples of an original data set. The point I wish to make is that b = 1–1.8 spans most of the range from random to highly aggregated distributions. Table 3 even presents cases where b = 2 is exceeded.

The above examples also cast doubt on the usefulness of b as a measure of aggregation. Table 2 provides cases where b ~ 1, but does not reflect a random distribution because a is greater than 1. In a population which is uniform at low densities, but random at high densities, b would be greater than 1 and would incorrectly indicate aggregation. Similarly, in a population where individuals were aggregated at low densities but random at high densities, b would be less than 1 and would incorrectly indicate aggregation. The answer to these contradictions is that b, by itself, is not a measure of aggregation. It reflects the way in which aggregation changes with density. Values of b = 0, 1, and 2 reflect that variance is independent of the mean, that variance is proportional to the mean, and that standard deviation is proportional to the mean, respectively. The relationship of aggregation to b is ambiguous.

Table 2 can be taken as evidence that aggregation usually increases with density in benthic samples, and fig. 1, 2, and 3 indicate that the trend may be similar within some, but not all, taxonomic groups, substrate types, and samplers. Tables 2 and 3 provide some evidence that the square root and logarithmic transformations are too extreme for most data sets. But the proposed transformation of X' = X^1/2

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is not entirely satisfactory either. In table 3, the square root transformation produces the lowest correlation between variance and mean in three instances, the proposed fourth root transformation is best in one instance, and the log transformation is best in three instances. Although the fourth root transformation is slightly better than the logarithmic transformation on the average, the reader would do well to accept this table as proof that benthic populations vary greatly in their degree of aggregation, and that each data set should receive individual appraisal and treatment.

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PRECISION VS. GENERALITY: A REPLY

Ecologists should strive to make precise predictions about nature. In any science, consistencies among sets of data collections must be found to build general theories. Because ecosystems are necessarily multivariate, theories of general applicability must initially sacrifice some precision in the name of general inference. Examples of this abound: Hemmingsen’s (1960) general theory of respiration rate, Rawson’s (1952) general theory of fish catch, Dillon and Rigler’s (1974) and Sakamoto’s (1966) theories of chlorophyll concentrations in lakes, Blueweiss et al.’s (1978) theories of life history parameters, Cornett and Rigler’s (1979) theory of hypolimnetic oxygen deficit, and Smith’s (1979) theory of phytoplankton production in lakes are all less precise than the specific data from which they were synthesized. The utility of general theories rests in their ability to make a priori predictions, and to describe interdependencies of variables. In spite of this, theories of general utility are often criticized for their inability to account for all residual variation.

In a recent article (Downing 1979), I sought general consistencies in the spatial distribution of the freshwater benthos of lakes and large rivers, and offered general rules which allow efficient transformation of benthos data and realistic planning of sampling programs. W. D. Taylor (1980) has suggested that I drew two subjective conclusions, in pursuit of generality, that were not supported by the analyses presented. These conclusions were (1) that the amount of aggregation is roughly the same over all taxa, sediments, and samplers, and (2) that the variance of a set of replicates ($s^2$) is predictable from the mean density ($\bar{x}$) with a high degree of precision. The strength of the second of these conclusions is obvious, since my overall regression accounted for 87% of the variation in $\log_{10}s^2$ (table 2), my equation to predict $\log_{10}s$ had an $F$ value of 5285 (table 4), and my equation to predict the standard deviation of benthos samples (eq. 4) performed better than any yet published (table 5). For this reason, I will dedicate most of this reply to the former question, regarding the similarity of aggregation among taxa, sediments, and samplers, and the appropriateness of $b$ (as in $s^2 = \bar{x}^b$) as a measure of aggregation. I hope to show that my minor subjective judgement allows major gains in the generality of application.

Before deciding if a measure of aggregation can be generalized among categories of data, one must decide upon the purpose for which that measure is useful. The question of the appropriateness of $b$ as a measure of aggregative behavior is a difficult one to answer since the only definition of aggregation that ecologists have is written in terms of capture probability (Taylor et al. 1978), not in terms of behavioral attraction. An aggregated population, then, is a population in which the population subcategories are more variable than random. This means that an aggregated population must have $s^2 > \bar{x}$. The variance that indicates that a population is aggregated varies with density; therefore, some index is needed so that the relative aggregation of populations of differing densities can be compared. Since sampling variance is almost always correlated with density, Taylor (1961) felt that comparisons between $s^2/\bar{x}$ regressions would be useful in determining whether animals had higher or lower variance than expected from their density (using $s^2 = \bar{x}$ as the null hypothesis). He suggested that the tendency toward the exponential rate of increase in $s^2/\bar{x}$ (i.e. $b$) might reflect the tendencies of animals to aggregate (i.e. greater or lesser departure from randomness). I agree with W. D. Taylor, however, that the entire expression for the density dependence of $s^2/\bar{x}$ is probably the most complete measure of spatial variability of organisms (i.e. $s^2/\bar{x} = \bar{x}^b$). The exponent $b$ would be a consistent predictor of variance only if $a$ were constant or positively correlated with $b$, but is nevertheless useful in calculating exact variance stabilizing transformations for sets of data. Thus, the null hypothesis of no difference in aggregation among groups can be accepted if $s^2/\bar{x}$ relationships $(s^2 = \bar{x}^b)$, calculated within groups, are not significantly different from that found in pooled data, and a universal transformation is valid if $b$, calculated within groups, does not vary significantly from the $b$ of pooled data.

The validity of my judgement that “aggregation is roughly the same” can therefore be determined by testing for significant differences between the general regression of $s^2/\bar{x}$ (all data) and specific regressions of $s^2/\bar{x}$ performed on more homogeneous data sets. The usefulness of a generalized transformation can be tested by examining the homogeneity of $b$’s calculated on relatively homogeneous data sets. I performed both of these tests on these benthos data (Downing 1979). The former test was performed by the method of Tsutakawa and Hewett (1977) which calculates the probability that the subgrouped data are distributed about the generalized regression line in the same manner as the balance of all replicate benthos data. This analysis showed that, when grouped as taxa or sediment types, only 12.7 and 6.7% of these categories deviated significantly from the generalized $s^2/\bar{x}$ regression. The effect of sampler size was shown (table 4) when replicate samples were grouped according to sampler (table 2), and was accounted for in predictive equations (eq. 4). This shows that, apart from sampler effects, the generalized regression

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1See also “Corrections to recent publications” in this issue.
of \( \hat{\sigma}^2 \hat{x} \) is an appropriate expression for the spatial variability of all but 10% of the categories of data.

Tests for homogeneity of \( b \) are shown in fig. 1–3. These figures show that subgrouped \( b \)'s deviate significantly from the overall \( b \) in 12.6, 5.5, and 17% of the categories. This shows, as I suggested, that my proposed universal transformation will not always be correct. However, ecologists do not often test the appropriateness of their transformation, but simply use the transformation that has generally been employed (e.g. logarithmic or square root). Since this practice is likely to continue, I feel that the transformation used most generally should be that which is most likely to succeed. For benthic data this seems to be \( X' = X^{0.25} \). Obviously, it would be best if each set of data was evaluated individually, but this is not always practicable.

In my analyses of benthos variability, I save sacrificed some precision for utility. Benthic animals are not always aggregated to the same degree but most deviations from this rule are correlated with sampler size. A universal transformation for benthos data will not always be correct but will be better than those formerly employed. Sampling variability is not completely predictable but my scheme provides the best predictions that we can make at this time, and requires no prior reconnaissance. It is my contention that this brief departure from absolute precision will allow us to perform significantly better ecological investigations of the benthos.

In conclusion, I would like to request the aid of other benthic ecologists in investigating the lack of homogeneity in aggregation about which W. D. Taylor is concerned. Larger sample sizes are required in all categories to test the hypothesis that apparent homogeneity in aggregation results from a lack of power in analysis. I repeat my request that anyone who possesses published or unpublished data on replicate benthos samples (either freshwater or marine) should forward them to me for inclusion in future analyses — John A. Downing, Department of Biology, McGill University, 1205 Ave. Docteur Penfield, Montreal, Que. H3A 1B1

**NEW LIGHT ON THE VARIANCE/MEAN VIEW OF AGGREGATION AND TRANSFORMATION: COMMENT**

Recent investigations into the variance/mean power function may help to clarify some of the issues raised by Downing (1979) and W. D. Taylor (1980). Although the subject material is not aquatic, the insight provided is generally applicable.

The original empirical “law” claimed that evidence from the literature showed spatial variance to be proportional to a fractional power of mean population density; that is, \( \hat{\sigma}^2 = am^b \), where \( \hat{\sigma}^2 \) and \( m \) are sample variance and mean, respectively. Some misconceptions no doubt arise from my premature suggestion that \( a \) might be wholly a sampling factor (L. R. Taylor 1961). I did not claim that \( b \) measures aggregation, as W. D. Taylor implies, but that it is an index which “remains the same for the same organism in the same environment” (L. R. Taylor 1965) because it results from “the partnership between the organism and the environment” (L. R. Taylor 1971).

Aggregation, however it is defined biologically, may differ at different densities, and the regression approach of the power function when written logarithmically (\( \log \hat{\sigma}^2 = \log a + b \log m \)) shows that, as W. D. Taylor rightly suggests, the exponent \( b \) measures the way variance changes with the mean; variance is density-dependent except when \( b = 1 \); then variance is proportional to the mean. However, the factor \( a \) must be known before the absolute variance/mean ratio can be specified for a given density. Also, the components of \( a \) must be known before the ratio can be extrapolated from one set of data to another, especially when samples are taken by different methods, although \( b \) remains the same in 95% of species examined (L. R. Taylor et al. 1980).

Also, since the specificity of \( b \) depends on a density-dependent interaction with the environment that can be modeled conceptually, if not specifically, by simple density-dependent movement (L. R. Taylor and R. A. J. Taylor 1977; R. A. J. Taylor and L. R. Taylor 1979), then sampling scale may have an effect. This is not the instantaneous spatial pattern effect of Paloheimo and Vukov (1976) referred to by Downing (1979), but a real change in individual behavior in response to fine-scale environmental change.

For example, the feeding behavior of the aphids Eucarapis punctipes and Myzus persicae is affected by the condition of the leaves of birch (Betula alba) and turnip (Brassica rapa), respectively. As leaves age through the season, the aphids become redistributed over the plant. When leaves are used as sampling units, there is a seasonal cycle in \( b \) (Wratten 1974; Hodgson 1978) because of the differential aging of the leaves. A more consistent result is obtained by taking a larger, spatially defined, unit, instead...
of the leaf which confounds unit with environment, and accumulating over the phenological period of change.

The dependence of $a$ on sampling methodology has been verified with different subsampling systems, including different methods of subsampling: for *Aphis fabae* in bean crops, $a$ changed and the exponent $b$ remained constant (L. R. Taylor 1970). In addition, an environmental effect on $a$ has been discovered in two aphids, *M. persicae* and *Phorodon humuli*. These aphids have different host plants in differing cycles of population growth during the season. In standardized samples from the different population cycles taken at the same fixed spatial coordinates, the different distributions of the host plants affected the total distributions of the aphids, changing $a$ but not $b$ (L. R. Taylor 1977; L. R. Taylor et al. 1979). In the same way, when birds were sampled separately in woodland and farmland using a standardized method, log spatial variance was accountable with very few exceptions to a linear relation with log mean density. 55 out of 111 species had single regressions but in forty-two species, the woodland and farmland data had parallel regressions, common $b$ with a different intercept $a$, in the two different environments (L. R. Taylor et al. 1980). This investigation also confirmed that the rarity of randomness, found previously in small-scale samples (L. R. Taylor et al. 1978), also occurred in large-scale spatial samples of nesting birds, flying moths, and flying aphids. The distribution of only one out of 471 species was not significantly different from random ($a = b = 1$) at all densities (L. R. Taylor et al. 1980) and we have found little evidence of regularity in any of the many samples examined.

Hence, in practice, systematic sampling that allows for localized or phenological changes in behavior confirms the original proposition. Regressions of log spatial variance on log mean density then have stable coefficients which may legitimately be treated as reflecting population parameters at a given spatial scale and used to develop specific transformations.

The power transformations were originally proposed for large-scale sampling surveys or programs where species' density might range over several orders of magnitude and the ad hoc square root and log transformations, commonly used for experiments with small mean differences, were expected to be biased (Healey and L. R. Taylor 1962). The reality of this bias has now been demonstrated. The distribution of sample means for 97 species of moths and 263 species of moths was highly skewed when the log transformation was used throughout, irrespective of the different variance/mean exponents, $b$, of the various species. In 91 out of the 360 species, regressions of variance on the mean remained highly significant after log transformation of original data (L. R. Taylor and Woold 1980). These were large-scale temporal samples, for which the log transformation is commonly used, but the power law applies equally as well to temporal as to spatial distributions.

Given the measured relationship between variance and mean for a given species in a given environment, transformation by power function is specific and repeatable. It may be approximated by an easier transformation over a limited range for convenience. In his table 3, Downing 1979 shows that for some low values of $b$, the log transformation fails, whilst for some higher values of $b$, the square root transformation is equally inappropriate. However, using the square root for the first two or three items and the log for the other three or four yields better results than the common transformation $X^{1.55}$; Elliott's (1977) recommendation to choose either square root or log, as is common practice, is therefore appropriate. Even so, the approximation should not be forgotten when subsequent models extrapolate the population beyond the data, as they commonly do.

Because the exponent $b$ is highly specific, ranging, for example, from 1.20 to 3.32 for different species within a single genus of moths (*Apamea*), so the lumping of species into larger taxa inevitably reduces the range. Lumping is usually done for unavoidable taxonomic or time-saving, rather than for statistical, reasons. The resultant transformations and analyses then strictly apply only to data sets with the same proportions of species at all densities; something not commonly found in practice. This may be unavoidable in large-scale survey sampling, but its hidden effect in subsequent analysis should not be overlooked. In the same way, within-species morphs of differing behavior ideally should not be grouped, although again sampling and identification problems may make this unavoidable. In this case, only vigilance in interpretation can prevent what appear to be statistically valid analyses and models, from becoming void. This is not a fault of the method but is inherent in the data.

For these reasons I agree with W. D. Taylor's main point, that a common transformation is unlikely to be adequate for all *benthos* species. Aggregation must differ between species, as indeed Downing demonstrates despite having lumped species within higher taxa. Differences might be less in the plankton; but selective behavior must be considerable on the bottom.

Although the word "aggregation" appears frequently in this context, it should perhaps be emphasized that there can be no statistical definition of it until it is biologically defined. W. D. Taylor's criticism of Downing's search for a common transformation, which many have tried to find, is not furthered by his artificial mathematical models. These have value only when they relate to something biologically real.

W. D. Taylor appears to misunderstand the variance/mean functional relationship in his attempt to argue from theoretical models to real distributions. Palaeoemo and Vukov (1976), quoted by Downing, do the same, with results that are not borne out in practice. Given the indisputable evidence now available for the observed relationship between variance and mean density, it is no longer reasonable to speculate about two-phase mosaics, or other model distributions, that do not incorporate this constraint. There is, in practice, no good biological reason to expect the same statistical frequency distribution to fit data for the same species at different densities (L. R. Taylor 1965). The origins of frequency distributions make this most unlikely. The prime, indeed, the only known statistical effect of any biologically defined aggregation is to increase variance. All proposed methods are based on this, whilst the effect on skewness and higher moments is unpredictable because no universal frequency distribution has yet been found. The other widely applied regression approach is that of Iwao (1968) based on Lloyd's (1967) mean crowding and Bartlett's variance/mean quadratic regression (Bartlett 1936). This approach also provides transformations, and it is associated with the negative binomial. The third regression approach is the negative binomial with a common $k$ (Bliss and Owen 1958). However, this so-called measure of aggregation, $1/k$, has a most curious relationship with density that seems biologically improbable (L. R. Taylor et al. 1979). Iwao's method seems to be valuable in model-
ing specific cases (Iwao 1977), and especially over small ranges of mean density. So may be all the measures given by Downing (1979) when they have been critically evaluated on real data. In the meantime the main value of the variance/mean power function is that its very wide application indicates some real underlying biological property that encourages a search for common processes and hopefully discourages the current trend towards the use of purely speculative theoretical models with little or no biological evidence to support them.

Even so, the main problem in field sampling is that emphasized by Elliott (1977); the need to compromise in sampling time, which leads to small samples and empty units. Too many zero counts make the most sophisticated sampling program useless, and small numbers of units per sample requires some prior knowledge of the variance to make realistic decisions about analysis. Since the coefficient of variation is dependent on the value of \( b \), and the number of sample units needed for a given level of precision also obviously increases with \( b \), it would be advisable to estimate \( b \) from preliminary samples before developing any extensive sampling program. Difficult as it may be to identify samples down to species, if there is any likelihood that this will be done at a later stage in the program, it is worth the effort initially to identify those species for which \( b \) is high; if they are essential to the program, they will set the level of sampling necessary to achieve its objectives. Also, such species will require a stronger transformation than the log. So it seems that Downing may be right, if only one transformation is feasible, to suggest the fourth root when the taxa are large and the data limited. In contrast, analysis of detailed or extensive sampling for single species will require a specific transformation, whilst the ad hoc choice of square root and log may well remain the most convenient compromise.

I should also point out that a sample with only a single individual, irrespective of the number of units, has \( S^2 = m \), i.e. \( a = b = 1 \), not 2 as stated by W. D. Taylor — L. R. TAYLOR, Rothamsted Experimental Station, Harpenden, Hertfordshire, England.


