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Measuring ecological stress: variations on a theme by R. M. Warwick

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Abstract. Two new indices are presented which reflect quantitatively the changes to be expected in an ecological community under stress, as previously described by R. M. Warwick. The indices summarize information which he presented graphically, and permit analyses of trends and inferential tests. We suggest that these indices should be tested with a wide variety of ecological time-series data in order to evaluate the feasibility of inferring ecological stress from static data.

Introduction

Ecological stress is an elusive and ill-defined concept, and consequently one which is difficult to measure. A few decades ago, a paradigm existed in which it was assumed that ecological communities tend toward a stable state of high diversity, and that various human-induced disturbances would drive them into a less-stable state of lower diversity. It was therefore assumed that an index of diversity could be used to indicate the degree to which a community was stressed, for example, by pollution (we use "pollution" and "stress" interchangeably throughout this paper). Rather than attempting to thoroughly establish the validity of relating diversity values to ecological stress by studying the behavior of such an index using time series of data from communities subjected to known changes in stress, many ecologists assumed that the concepts were valid and used the indices without adequate prior testing (Green 1979). Recently, it has been shown that the relationships between diversity, stability, and stress are far more complex than previously imagined (May 1973, Connell 1978, Huston 1979). Few people now assume that ecological stress can be inferred from diversity alone.

Warwick (1986) summarized prevailing views into a new conceptual model for predicting changes in a macrobenthic community being gradually more polluted. The model includes the following assumptions: (1) Prior to being stressed, the community tends towards an equilibri-

um composition. (2) As it approaches equilibrium, the biomass becomes dominated by a few species with individuals that are large but few in number. (3) The species dominating the biomass approach a state of equilibrium with available resources. (4) Numerical dominance is maintained by species which are small. This results in a more even distribution of numbers of individuals among species than biomass among species. (5) The smaller species are out of equilibrium with available resources (it is implied that this helps to explain Assumption 4). (6) The abundances of the smaller species are subject to more stochastically controlled variation than the larger species (perhaps because of Assumption 5, but this is not usually stated). (7) Under moderate pollution, the large dominants are eliminated, resulting in less difference between evenness in terms of biomass and numbers. (8) Under severe pollution, communities become numerically dominated by a few very small species. (9) Under severe pollution, the few remaining large species will contribute proportionally more to the total community biomass relative to their abundance than will the numerically dominant small species. The net effect of Assumptions 8 and 9 is that the biomass will be more evenly distributed among species than numbers of individuals are.

Each of these assumptions is debatable. For example, the assumption that communities generally tend toward an equilibrium state has been questioned by Connell and Sousa (1983). Few studies of community behavior have been conducted across time-frames which are appropriately long relative to the life spans of the organisms in the community. The same could be said for evaluating many of the other assumptions listed here. However, the fact that they are presented in a meaningful context can serve to focus research on their validity, and the assumptions have the admirable quality of being testable in a falsifiable manner.

Ultimately, the utility of the model implied by Assumptions 1 to 9, must be determined from its ability to predict changes in data sets of known property. The graphical approach of Warwick (1986) involves presenting community structure data in the form of *k*-domi-

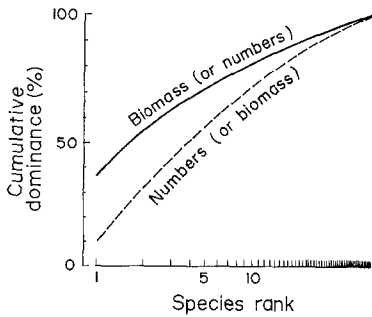


Fig. 1. Schematic k -dominance curve for species biomass and number. When stress is low, upper curve refers to biomass and conversely, moderate stress results in overlap of the two curves

nance curves, where k refers to a set of species used to describe dominance (Lambhead et al. 1983). The graphs consist of a logarithmic x -axis with the ranks of species by abundance, and a y -axis along which are plotted the cumulative percent abundances and biomasses by species (Fig. 1). An unpolluted community is expected to result in a curve for biomass which lies above that for numbers. A community from a polluted situation should result in a numbers curve which is above the biomass curve. The analytical technique is referred to as the "abundance biomass comparison" (ABC) method (Warwick et al. 1987).

The graphs have the advantage of revealing aspects of the data which would be obscured in a summary index. However, the interpretation of the graphs is subjective in many cases. It would be difficult to use a series of such graphs to discern trends in long data sets and to verify the trends using inferential testing. We have developed two indices which summarize the comparative data on biomass and number evenness needed to construct such graphs in a manner which is objective and facilitates statistical analysis.

Difference in area by percent (DAP)

In practice, a comparative interpretation of two similar ABC graphs would involve visually comparing the area between the curves to determine which graph represents the more polluted situation. We suggest that a more objective procedure would be to reduce each graph to a single number representing the area between the numbers and biomass curves.

Smoothing the curves is not necessary, because this would not add to the precision of the assessment. Instead, we treat the data points as if they were connected by discrete, straight line segments. Integrations can then be performed in a variety of ways, including counting squares on graph paper. We use a microcomputer program (available from the authors) which calculates the area under each set of discrete-segment "ogives", and then subtract the difference. The difference is then expressed as a percent of the total area of the graph, by dividing by the natural log of the number of species, i.e.

$$\text{Biomass area} = \sum_{i=1}^{s-1} [C_i + (0.5 \times Y_i + 1)] \times [\ln(i+1) - \ln i], \quad (1)$$

$$\text{DAP} = (\text{numbers area} - \text{biomass area}) / \ln s, \quad (2)$$

where s is the number of species, C_i is the cumulative biomass up to the species of abundance rank i (beginning with the highest ranked species on the x -axis), and Y is the biomass of a given species. The numbers area is calculated analogously, with counts of individuals instead of biomass.

The DAP index ranges from -1 to 1 , with high values indicating the stressed conditions.

Shannon-Wiener evenness proportion (SEP)

There are several well-established indices which express ecological evenness. The model of Warwick (1986) specifically mentions evenness as the characteristic of interest. One of the most commonly used indices of evenness is that based on the Shannon-Wiener index (Pielou 1977), i.e.

$$E = H' / \log s, \quad (3)$$

where

$$H' = -\sum P_i \log P_i, \quad (4)$$

and

$$P_i = X_i / N. \quad (5)$$

Here, X_i is the abundance of species i (in any order), and N is the total abundance in the sample.

A reasonable index of ecological stress derived from Warwick's two-curve model would then be

$$\text{SEP} = E_{\text{biomass}} / E_{\text{numbers}}. \quad (6)$$

Because the number of species in a sample is the same whether one measures numbers or biomass

$$\text{SEP} = H'_{\text{biomass}} / H'_{\text{numbers}}, \quad (7)$$

which is relatively simple to calculate.

Warwick (1986) mentioned that diversity indices based on biomass data cannot be compared with those based on counts. However, provided that the diversity indices are standardized to abundance, as is the case in H' , and that the diversities are compared as a ratio yielding another index, then we see no reason for concern.

Pielou (1977) recommends the use of an evenness index based on Brillouin's index of diversity over that based on the Shannon-Wiener index. One objection to the latter is the general inability of ecologists to determine the actual number of species in a community. In the case of the SEP index, the number of species cancels out, and is not a problem. Other objections to the Shannon-Wiener index involve the tendency of the index to under-estimate the true value in the sampled area. Our use of the SEP index, however, assumes only that the ratio of number and biomass diversities in a sample do not differ significantly from the ratio found in the community. While this appears to be a reasonable assumption, it warrants further investigation. The computational complexity of the evenness index associated with Brillouin's index limits its utility by ecologists with limited access to computers and specialized software.

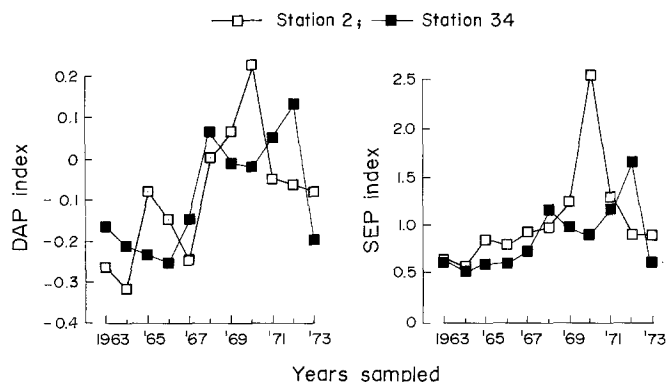


Fig. 2. Trend of stress at Stns 2 and 34 of Pearson (1975). Note similar trends for both DAP (difference in area by percentage) and SEP (Shannon-Weaver evenness proportion) indices

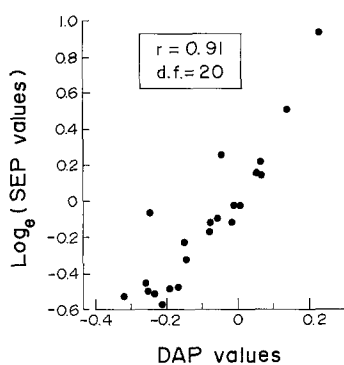


Fig. 3. Relationship between values of the DAP and SED indices (from Fig. 2)

Comparative analyses

The data of Pearson (1975) were analyzed with the two indices for comparison with the graphical analyses performed by Warwick (1986) on the same data. The data represent repetitive samplings made for 11 yr (1963, 1973 inclusive) at two stations in adjacent lochs in Scotland [Stns 2 and 34 of Loch Linnhe and Loch Eil, respectively, from Pearson (1975)]. The two lochs are connected by a waterway along which a pulp-mill began discharging effluent in March 1966. The flow was maintained at 10 to 14 tons d^{-1} from 1967 to 1969, increased to a maximum of 30 tons d^{-1} in late 1970, and was reduced again to 10–14 tons d^{-1} in the autumn of 1971 until 1973. Samples each represent a pooling of five grab samples in the spring of each year from 1963 to 1973. Warwick's (1986) graphical analysis suggested low stress levels from 1963 to 1967, moderate levels from 1968 to 1970, gross pollution in 1971 and 1972, and a return to low stress levels in 1973 in one of the two stations. The other station appeared not to have recovered by 1973, and still showed moderate levels of stress.

Fig. 2 shows results of analyses by DAP and SEP indices. Warwick's results are confirmed by both indices. The DAP index showed a greater range of variation among low, medium and high levels of pollution. Fig. 3

is a scatter diagram of natural log SEP values against DAP values. It can be seen that the relationship between the two is log-linear.

Conclusions

The indices presented here are not intended to be used in static analyses of community structure information as a primary means of determining stress effects. They are intended, instead, to provide a means for testing the reasonable model for community changes under stress outlined by Warwick (1986). To facilitate this, we are currently investigating the applicability of both within and between sample variability measures to the indices. The model may be valid for some classes of macrobenthic communities and stresses and not others (Gray et al. 1988). Also, it is conceivable that the model is applicable to stressed communities other than macrobenthic. For example, it would be useful to monitor tropical, multispecies fisheries which draw from a large species pool, and where clear relationships between individual sizes, population number, biomass and fishing pressure (=stress) have been demonstrated (Pauly 1979, 1988, McManus 1985). However, the model must be tested with a broad range of examples before the limitations of its utility can be clearly established. Only then can these or similar indices based on the model be confidently applied to the analysis of isolated community samples.

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