

Neutral model analysis of patterns of marine benthic species diversity

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ABSTRACT: Caswell (1976) proposed a neutral model which calculates a theoretical diversity for a sample of a given number of individuals and species assuming no biological interactions between species. Disagreement with the neutral model predictions have been suggested as a method of detecting disturbance or stress. To test these theoretical considerations, 98 samples of marine benthic organisms were subjected to neutral model analysis. Deviation from the predicted diversity was generally found to be negative – less diverse than expected. Where disturbance was known to have occurred, spatial or temporal variations in the degree of deviation were in accordance with a hypothesis of diversity based on a combination of the Intermediate Disturbance Hypothesis (Connell 1978) and the General Hypothesis of Diversity (Huston 1979). Artificially created log-normal patterns of species abundance distribution gave a diversity greater than that predicted by the neutral model. But in no cases where the diversity of actual samples exceeded the neutral model prediction were the species abundance distributions log-normal.

INTRODUCTION

There is continuing debate as to whether diversity is or is not any longer to be considered a valuable concept in theoretical population biology (Osman & Whitlatch 1978, Thomas & Foin 1982). The arguments are often highly technical, involving mathematics well beyond the grasp of most practising ecologists. But whether or not it will ever be possible to fully understand the processes responsible for any particular form of species assemblage, there exists a more practical question. Is there a reliable method of assessing patterns of species abundance which would allow us to test predictions about what we might expect to find in any given situation?

Various measures of diversity have been tried: simple indices such as the Shannon-Wiener information function; fits to empirical models such as the log-normal distribution; simple pictorial representations of relative species abundance such as the *k*-dominance curves. All have been found to be wanting in various ways, usually through being either too insensitive or too sample-size dependent (Lamshead et al. 1983, Shaw et al. 1983, Platt et al. 1984, Lamshead & Platt in press). In this paper we wish to consider a fourth alternative – neutral model analysis and in particular Caswell's (1976) neutral model.

Neutral models attempt to eliminate all those forces which might play a part in explaining an observed pattern of species abundance, such as interspecific biotic interactions or differential responses to the environment. The neutral model is then used to generate a predicted pattern, given the total number of species (*S*) and individuals (*N*) in a sample, against which to compare the observed pattern. Theoretical population biologists use these models to attempt an explanation of observed patterns through falsification of sets of plausible neutral hypotheses. It should be noted that there has been some debate about whether certain models are truly neutral (e.g. Ugland & Gray 1983, Caswell 1983): we defer comment at this point. Here we are simply interested in the neutral model as an alternative, relatively sample-size independent measure of diversity. As a starting point in its evaluation, we will ascertain whether or not the technique can detect differences in diversity which can be shown to be statistically significant. We will then consider the results in relation to a dynamic hypothesis of diversity and finally in relation to the log-normal hypothesis of species distributions.

In this paper, we use the term 'disturbance' which we define as follows. Disturbance is the process which occurs when any physical or biological agent acts to reduce population size, either by a direct biocidal

action or by some indirect effect on population growth rates. It is important to note that we are only considering non-selective disturbance. The effects of selective disturbance (such as selective predation) will be situation-specific and hence effectively unpredictable by any general theory.

MATERIALS AND METHODS

Neutral model analysis. We used the neutral model computer program adapted by Caswell (1976) from the genetic model developed by Ewens (1972). The program calculates the observed diversity (H') of the assemblage and a theoretical diversity (EH') for a sample with the same N and S . From this, a deviation statistic (V) is calculated by subtracting EH' from H' and dividing by the standard deviation of EH' . When $V = 0$, the sample is deemed to have been derived from a 'neutral' assemblage. Where V is greater or less than 0, the assemblage is not neutral: positive values result from excess equitability, negative values from excess dominance. So where hereafter we refer to samples being 'more diverse' or 'less diverse' than other samples we mean with reference to this theoretical diversity, EH' , and not to absolute values.

One of the problems with the neutral model is purely computational: because of the iterative nature of the program, and despite using exceptionally powerful main-frame computers, we were unable to run some of the samples. This occurred in our case where N was greater than about 9,000. There are also major problems with attempting to artificially reduce data for this type of analysis: we refrained therefore from doing so.

Data sets used. The following 103 data sets were analysed. All the biological samples were good non-amalgamated data where we were reasonably confident that the circumscribed organisms had been exhaustively identified to species.

(1) 16 marine nematode samples from various clean and sewage-contaminated intertidal fine sand beaches, collected contemporaneously from the Clyde Sea area, Scotland (Lamshead 1983). Samples were collected from the low tide mark at 6 different locations specifically chosen to be as similar as possible in terms of the environmental parameters. Hereafter these samples are referred to as the 'Clyde nematodes'.

(2) 36 marine nematode samples from an intertidal sandflat in Strangford Lough, Northern Ireland. The samples were collected at monthly intervals from high, mid and low tide stations located on a single transect (Platt 1977). Hereafter these samples are referred to as the 'Strangford nematodes'.

(3) 16 subtidal macrobenthos samples from stations in Loch Eil (Sta. 2) and Loch Linnhe (Sta. 34), Scotland,

collected annually from 1963 to 1973 (Pearson 1975). Both stations were about equidistant from the point of discharge from a pulp mill, which began discharging in 1966, peaked in 1970 and reduced in subsequent years. Hereafter these samples are referred to as the 'macrofauna'.

(4) 30 deep-sea foraminiferan samples from 6 cores taken contemporaneously at 1,320 m depth in the Porcupine Seabight, collected with the Scottish Marine Biological Association's multiple corer, subsampled with 3.5 cm cross-sectional area syringe to a depth of 5 cm and sectioned at 1 cm depth intervals (unpubl. data from Dr. A. Gooday). Hereafter these samples are referred to as the 'foraminiferans'.

(5) 5 computer-generated sets of artificial data. Two were designed to have a log-normal distribution, 1 a log-series and 2 based on a log-series but where dominance was subsequently increased.

RESULTS

Table 1 shows the V -statistics for the Clyde nematodes from the clean (Sta. 1 to 3) and contaminated (Sta. 4 to 6) locations. V was < 0 except in 2 of the Sta. 4 samples.

Table 1. Neutral model V -statistics for marine nematode assemblages from various low tide stations in the Clyde estuary (from Lamshead 1983)

Uncontaminated samples									
1A	1B	1C	2A	2B	2C	3		Mean	
-1.05	-1.28	-0.65	-2.45	-1.00	-1.42	-0.52		-1.20	
Contaminated samples									
4A	4B	4C	5A	5B	5C	6A	6B	6C	Mean
+1.30	+0.59	-1.41	-1.15	-0.08	-0.23	-0.38	-0.08	-1.22	-0.03

Table 2 shows the V -statistics for the Strangford nematodes. Total nematode numbers at the mid and low tide stations showed no particular seasonal trend. However, at the high tide station (Fig. 1) there was a clear population increase in May/June followed by a drastic reduction in July and a subsequent return to the overwintering level. This was reflected in the V -statistics, as will be discussed below.

Table 3 shows the V -statistics for the macrofauna: absence of data is due to huge sample sizes.

Table 4 shows the V -statistics for the foraminiferans. The samples were extremely rich in species, with a mean S and N for the 0 to 1 cm layer of 91 and 350 respectively.

Table 5 shows the V -statistics for the artificial data,

Table 2. Neutral model V-statistics for marine nematode assemblages sampled monthly at high, mid and low tide on a sandflat in Strangford Lough, Northern Ireland (from Platt 1977)

Month	High tide	Mid tide	Low tide
Jan	-4.16	+0.23	-0.59
Feb	-1.01	+0.75	+0.08
Mar	-0.64	-0.57	-0.07
Apr	-1.56	-0.06	-0.57
May	-0.70	+0.62	-1.22
Jun	-0.77	-1.18	+0.64
Jul	-4.18	+0.15	-2.12
Aug	+0.26	+0.20	-0.32
Sep	-1.64	+0.06	+0.80
Oct	-1.47	-2.00	-0.65
Nov	-2.02	-0.14	-1.34
Dec	-5.60	-1.46	+0.30
Mean	-1.96	-0.28	-0.42

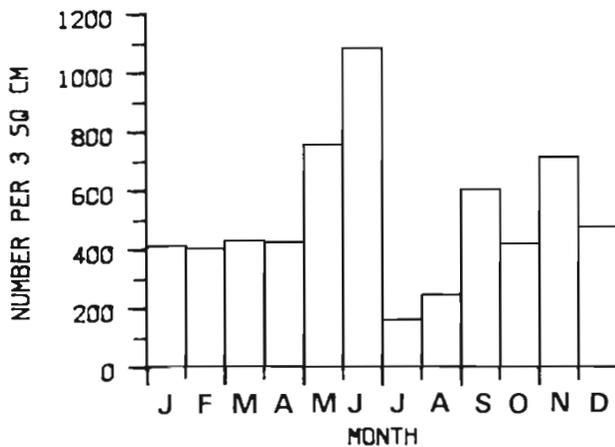


Fig. 1 Nematode population density per month at the high tide station in Strangford Lough, Northern Ireland (from Platt 1977)

Table 3. Neutral model V-statistics for macrobenthic data from Loch Eil (Sta. 2) and Loch Linnhe (Sta. 34) (from Pearson 1975). Contamination from a pulp mill began in 1966 and peaked in 1970

Year	Sta. 2	Sta. 34
1963	+0.78	-1.63
1964	+2.65	-0.50
1965	+0.67	+0.79
1966	-	+1.95
1967	-0.32	+0.30
1968	-1.35	-2.63
1969	-2.61	-0.80
1970	-	-1.35
1971	-	-
1972	+0.40	-
1973	-	+0.13

Table 4. Neutral model V-statistics for deep-sea foraminiferans from the Porcupine Seabight, North Atlantic. Six 5 cm deep cores (A-F) sectioned at 1 cm intervals

Depth cm	A	B	C	D	E	F	Mean
0 to 1	-3.33	-3.13	-2.62	-2.89	-2.68	-4.37	-3.17
1 to 2	-2.85	-2.63	-2.09	-0.67	-2.68	-1.03	-1.99
2 to 3	0.00	0.00	-0.65	-1.13	-1.50	-0.13	-0.57
3 to 4	-1.36	+0.83	-1.53	-1.95	+0.33	-0.41	-0.68
4 to 5	-0.43	-1.27	+0.31	0.00	-1.89	-1.37	-0.78

Table 5. Neutral model V-statistics for 5 sets of artificial data. Sets 1 and 2 had a log-normal distribution of species abundances (with increased dominance in Set 2), Set 3 was a log-series and Sets 4 and 5 were based on the log-series but had an enhanced dominance. N: total number of individuals; S: total number of species; *d*: abundance of commonest species as a percentage of total sample

Set	V	N	S	<i>d</i>
1	+2.34	255	24	12.6
2	+1.06	220	24	28.6
3	+0.05	285	23	28.8
4	-1.09	367	23	44.7
5	-1.50	400	23	49.3

all of which had about the same S and N but where the percent abundance of the most common species was varied.

DISCUSSION

The neutral model

The appropriate null hypothesis to begin with is that disturbance of natural species assemblages will have no effect on the relative numbers of species as measured by the Caswell neutral model. Let us look at the various data sets to see if this is falsifiable, beginning first with the 'spatial data' (Clyde and Strangford nematodes; foraminiferans) and then the 'temporal data' (Strangford nematodes; macrofauna).

The V-statistics of the Clyde nematodes vary between -2.45 and +1.30, although only 2 are positive. But the mean of the clean samples (-1.20) is significantly different from that of the sewage contaminated samples (-0.30) at $P = 0.05$. We can find no factor other than the pollution that can explain this result. So we could conclude that the clean assemblages are significantly *less* diverse than those of contaminated sites.

The mean V-statistics of the mid and low tide Strangford nematodes (-0.28 and -0.42) are not significantly different but both are significantly different

available to the scientific community. Also, fashion in the manipulation or interpretation of data may change but the raw data will remain. Second, we have made no mention yet about how the V-statistic compares as a diversity or equitability measure with other approaches in order to justify the investment in computer time, nor have we discussed the point about the neutral model being relatively sample-size independent. We wish to reserve these points for another paper on the neutral model we have in preparation.

The log-normal hypothesis

There is a hypothesis that the species abundance distribution patterns of undisturbed assemblages of organisms fit the statistical model known as the log-normal (Gray 1981). We had hoped that we had effectively falsified this hypothesis (Shaw et al. 1983, Lamshead & Platt in press) but publications containing ecological analyses based on this hypothesis continue to appear. Since the neutral model provides a method of searching for possible log-normal distributions we would like to make the following observations.

We interrogated the neutral model with several artificially created data sets. Of course, a log-series gave a V-statistic close to zero (Table 5, data-set 3). When we

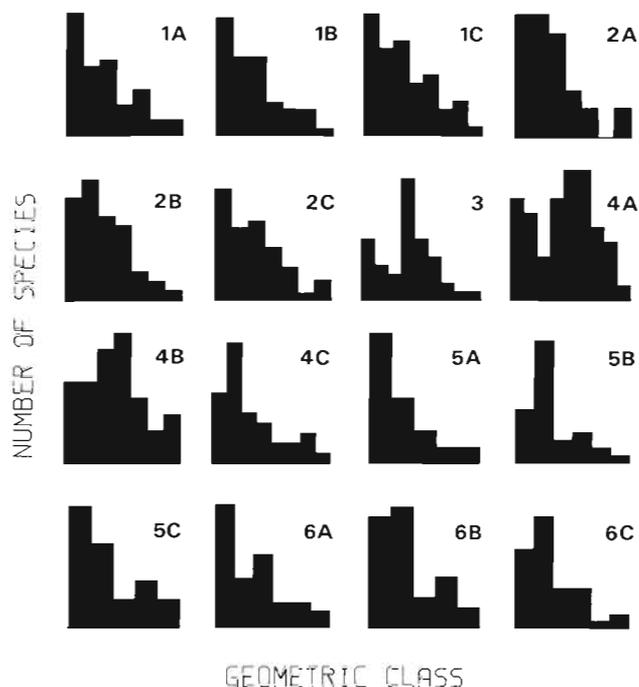


Fig. 3. Log-transformed species abundance data of the Clyde nematodes from the stations listed in Table 1. The x-axis is $\times 2$ geometric class and the y-axis is number of species; absolute values irrelevant

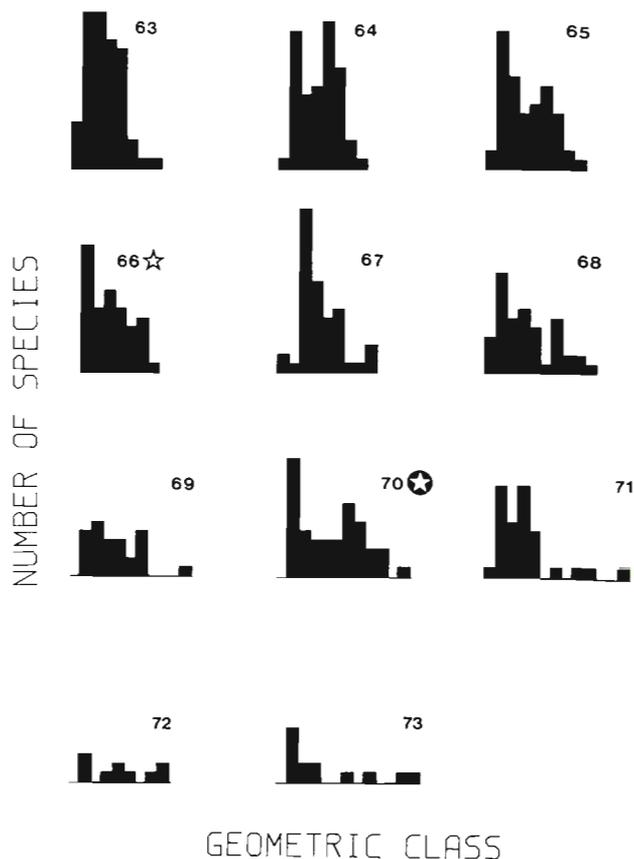


Fig. 4. Log-transformed species abundance data of macrofauna from Sta. 2 for the years listed in Table 3. Axes as in Fig. 3

artificially altered data based on a log-series to enhance the dominance, V shifted negatively; the greater the dominance the more negative the value (Table 5, data-sets 4 & 5). However, log-normal distributions always gave a positive value provided they were not over-dominated by a few species. The lower the dominance the more positive the V (Table 5, data-sets 1 & 2).

An analysis of the explanation for the formation of log-normal distributions indicates that they are most likely to occur in a post-disturbance situation where there has been unrestricted growth (Lamshead & Platt in press) and where diversity is increased (between points D and E in Fig. 2). We therefore looked for appropriate instances in our data, such as the Strangford nematode high tide August value (Table 2), the Clyde nematodes at Sta. 4A and 4B (Table 1) and the macrobenthos Sta. 2 values (Table 3). In no cases were the log-transformed species abundance curves demonstrably log-normal. The appropriate curves for the Strangford nematodes are in Lamshead & Platt (in press), those for the Clyde nematodes and macrobenthos are shown in Fig. 3 & 4 respectively.

Log-normals, therefore, cannot even be detected in those assemblages where they might be expected and the necessary uninhibited growth situation is indicated by the neutral model. This may be because the required randomness is never present in nature. In other words, even in uninhibited growth assemblages there are always some overriding factors. Alternatively, log-normal distributions might be present in post-disturbance assemblages but they cannot be detected because of the low number of points on the log-transformed curves (Platt et al. 1984). Preston (1962) suggested that a sample of 40 000 individuals and 200 species is adequate to establish log-normality. Despite being considerably larger than most *genuine* benthic samples, this still gives at most a 16 point curve.

In summary: (1) the hypothesis that a log-normal distribution of species abundances is normally to be expected in nature is falsified; (2) the hypothesis that a log-normal distribution of species abundances is found in post-disturbance situations is probably untestable.

CONCLUSIONS

(1) The deviation statistic V derived from Caswell's neutral model appears to be a sensitive tool for the elucidation of the effects of disturbance on species abundance patterns.

(2) The combined diversity hypothesis based on Connell's (1978) and Huston's (1979) work was tested by running 98 benthic samples on Caswell's neutral model. In all cases, detailed examination of the V -statistics failed to provide instances where the hypothesis could be falsified.

(3) Artificial log-normal species abundance distributions produce a positive V -statistic. But in no cases where positive V -statistics were found in real samples were the species abundance patterns unequivocally log-normal.

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