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THE IMPACT OF DISTURBANCE ON MEASUREMENTS OF VARIABILITY IN MARINE NEMATODE POPULATIONS

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ANALYSE DE LA VARIANCE
DISTRIBUTION SPATIALE
POLLUTION
PERTURBATIONS
DE L'ENVIRONNEMENT
NÉMATODES MARINS

RESUME – Le rôle de la répartition en agrégats dans la régulation de la biodiversité est l'un des thèmes majeurs de l'écologie ; des théories récentes, telle celle de la mosaïque spatio-temporelle, ont souligné l'importance des perturbations dans la création d'agrégats en tant que processus de structuration des communautés benthiques marines. De récents articles ont suggéré que l'utilisation de mesures paramétriques de la variabilité pouvait rendre compte de l'impact de perturbations naturelles ou anthropiques dans toute étude de la répartition en agrégats. Nous avons voulu contrôler ces assertions à partir de cinq séries de données concernant des Nématodes marins de milieux abyssaux et littoraux soumis à des perturbations quantifiées. Il apparaît que la variabilité entre échantillons, mesurée par le rapport variance sur moyenne des abondances spécifiques, est liée à la perturbation du milieu. Néanmoins, des données complémentaires sur les processus intervenant sur la distribution agrégative à petite échelle sont nécessaires pour utiliser cette approche en test de pollution.

VARIANCE TESTING
SPATIAL DISTRIBUTION
POLLUTION
DISTURBANCE
MARINE NEMATODES

ABSTRACT – The role of patchiness in the maintenance of biodiversity is a major theme in ecology and modern theories such as the spatial-temporal mosaic theory have stressed the importance of disturbance in the creation of patchiness as a process structuring marine benthic communities (Grassle and Morse-Porteous, 1987 ; Grassle, 1989). Some recent papers (Lamshead and Gooday, 1990 ; Rice and Lamshead, in press ; Warwick and Clarke, in press) have suggested that investigation of patchiness by parametric measures of variability can be used to assess the impact of natural and anthropogenic disturbance. We test these assertions on five marine nematode data sets from deep-sea and shallow-water environments subjects to known levels of disturbance. We conclude that variability between samples as measured by the variance/mean ratios of the abundance of the individual species in communities is linked to environmental disturbance. However, more information on the processes influencing small-scale patchiness under different disturbance regimes is required before this could be recommended as a reliable pollution test.

INTRODUCTION

The spatial and temporal variability in biological populations is a central area of interest in ecology (Andrewartha and Birch, 1954 ; 1984 ; Begon *et al.*, 1986). However, the way variability is measured can considerably influence ecological interpretations (Taylor, 1961) such that there is as much interest in the measurement of variability as in the type and amount of spatial variability generated by various ecological processes (*e.g.* Hanski, 1990 ; Taylor, 1984 ; Taylor and Woiwod, 1982).

Patchiness is the most common manifestation of spatial variability and disturbance is now considered to be one of the primary processes influencing patchiness, and hence diversity and community structure. If disturbance is the main cause of patchiness, this offers the prospect of using spatial variability to assess natural and anthropogenic disturbance (Lamshead and Gooday, 1990). In this paper, we test the use of some measures of patchiness based on the parametric variance which have been suggested for the detection of disturbance (Rice and Lamshead, in press ; Warwick and Clarke, in press). We compare five

nematode data sets with different, known levels of disturbance to see whether these measures of variance are good assessors of disturbance.

TESTED HYPOTHESES

Using the five data sets it is possible to test three hypotheses :

1) That more species in a deep-sea community are significantly aggregated in a more disturbed system than a less disturbed system (Lamshead and Gooday, 1990 ; Rice and Lamshead, in press).

2) That fewer species would tend to be aggregated in a shallow-water community than a deep-sea community due to the high levels of disturbance experienced in coastal seas.

3) That the rate of aggregation with abundance for marine communities increases with higher levels of disturbance (Warwick and Clarke, in press).

CHOICE OF DATA SETS

A potential source of error that cannot be avoided is the interaction between sampler-size and organism patch-size. The measured variance not only measures the degree of aggregation in a patch but also the size of the patch relative to the sampler : a sampler hugely larger than the patches will tend to sample many patches together, reducing measured variability, and a sampler considerably smaller than the patches risks replicates being taken from within a single patch, also reducing measured variability. Employing a fixed core size for all habitats is not a viable strategy partly because of sediment characteristics, partly because abundances change markedly from place to place, and partly because we have no evidence that nematode patches are the same size in all environmental conditions. How much of a problem sample-size/patch-size interactions are in practice is unclear.

Choice of data sets is critical for comparisons of variance because estimates of variance are directly influenced by sampling strategy. Taylor (1961, 1984) introduced the power law $S^2 = aM^b$ for the variance (S^2) and mean (M) of population samples where "a" and "b" are constants. It was originally considered that, although "a" was sample-protocol dependent, "b" described the aggregation of the organisms and was thus independent of sample protocols. However, Sawyer (1989) demonstrated that "b" was also influenced by sample protocols so all variance analysis re-

sults reflect sampling strategy as well as underlying organism distributions. It is, therefore, necessary to standardise sampling protocols before any meaningful comparisons can be made between different populations. Accordingly, we investigate a single taxon, marine free-living nematodes, which have all been collected by similar specialist meiofauna corers, either hand held for the shallow-water samples (Platt and Warwick, 1988), or remote for the *Alvin* (Thistle and Eckman, 1990) and multiple corer deep-sea samples (Barnett *et al.*, 1984), which should function with similar efficiency. Six, independently sampled, replicates were taken for each site.

Five sets of data met the criteria for this analysis, including two matched pairs of disturbed/control stations. The criteria are : (i) same organisms, (ii) similarly efficient samplers, (iii) similarly efficient extraction technique, (iv) standardized taxonomy, particularly of unknown species, and (v) known disturbance regime of the site sampled. The first matched pair is the DEEPSEAS stations in the north-east Atlantic (Rice and Lamshead, in press). The 4,856 m deep northern Porcupine Abyssal Plain site (PAP) at 48°50'N : 16°30'W is subject to a major seasonal input of phytodetrital material. The 4,850 m southern Madeiran Abyssal Plain site (MAP) at 31°N : 21°W has an organic supply which is both lower and less periodic. These stations were selected to test for the effect of different food regimes on abyssal fauna. The multiple core sampler employed had an internal diameter of 5.7 cm.

The third deep-sea data set comes from the San Diego Trough (SDT) from a 1,050 m station at 32°52'N : 117°45.5'W which is described in Thistle (1978). SDT is a physically undisturbed site with high productivity by deep-sea standards but the meiofauna are subject to biogenic disturbance from the abundant macrofauna (Thistle and Eckman, 1988 ; 1990 ; Eckman and Thistle, 1991 ; Thistle *et al.*, 1993 ; Lamshead *et al.*, submitted). It is difficult to scale the disturbance at SDT against PAP, biogenic disturbance against a seasonal input of food. However, we are on firmer ground in concluding that SDT experienced higher levels of disturbance than MAP, which could be used as a control in a paired comparison. The *Alvin* corer had a 6.6 cm internal diameter.

Finally, the second matched pair were shallow-water stations from the Clyde inland sea area. These stations are described in Lamshead (1986). Briefly, the samples were taken from two geographically close areas, Etrick Bay (EB) and Ayr Bay (AB), which were similar in the major ecological parameters (salinity and grain size) except that Ayr bay suffered from sub-catastrophic contamination from industrial and sewage effluent. The hand-corer employed had a 2.2 cm inner diameter.

The two matched data sets employed here (MAPvPAP and EBvAB) were collected during projects specifically designed to test disturbed sites against reference sites so the reference sites are as valid controls as may be practically achieved. Even so, they suffer from the usual pseudoreplication problems associated with field ecology in a marine environment (Green, 1979; Hurlbert, 1984). Briefly, it is extremely difficult to set up randomised plots with differing treatments in the marine environment because the water medium tends to disperse the treatment.

In addition to the two matched sets, MAP can be used as a reference station for all four data sets on two grounds. First, it is a low organic supply, unperiodic, physically undisturbed station and it can confidently be concluded that it experiences lower levels of disturbance than any of the other stations. Second, it represents the most common nematode habitat, given that a significant portion of the globe is covered by this type of environment.

STATISTICAL ANALYSIS OF VARIANCE

The most direct way to assess variability is to quantify it with a robust and mathematically tractable measure and explicitly test the significance of comparisons. The measure of variability used most is the variance of some measure of abundance in samples, or associated statistics such as standard deviation. There are several methods for explicitly testing variance, many of which have been reviewed by Van Valen (1978) and Zar (1984). However, most require specific types of data which limits how they can be used. Hence, in this paper we consider only those which are least affected by sample protocol and have been suggested for assessing the impact of disturbance on populations of marine organisms.

Lambshead and Gooday (1990) used the simple F-test, the most standard method, to show that deep-sea Foraminifera samples from the Porcupine seabight are more variable after a phytodetritus drop. The problem with the F-test is that it is extremely sensitive to deviations from normality (Box, 1953; Pearson and Pleese, 1975) and distributions of organisms can deviate considerably from normality (Taylor, 1961; Van Valen, 1978). For this reason this method is not recommended and is not employed here.

The first approach we used was variance to mean ratios (Hessler and Jumars, 1974; Jumars, 1975, 1976; Gage, 1977; Thistle, 1978). The variance to mean ratios multiplied by the degrees of freedom (number of samples-1) gives a good estimate of the Chi Squared statistic. Aggregated or

regular distributions can then be tested for using the Chi Squared distribution, with 5 degrees of freedom ($n-1$). A probability of $< 2.5\%$ indicates significant aggregation, $> 97.5\%$ indicates a regular distribution, and any other result indicates a distribution that cannot be distinguished from random.

The results from the previous analyses listed mostly indicated randomly distributed organisms but Jumars and Eckman (1983), in their seminal paper, note that the low abundances in the deep-sea communities analysed by these authors make a Type II error likely, i.e. the resolving power of the test becomes so low that non-random distributions cannot be distinguished from random. This is a strong argument for turning to a taxon with abundant species, such as marine nematodes. Rice and Lambshead (in press) followed Jumars and Eckman (1983) in plotting variance to mean ratios against mean for the nematode assemblages at MAP and PAP. Even using such an abundant taxon many rare species have to be eliminated from the analysis as they drop below the resolving power of the test. Rice and Lambshead adopted a sum of ten animals in the six cores as the lower limit for testing. They reported that only 5 species (28% of the total species tested) were significantly aggregated at the undisturbed site (MAP) while at disturbed PAP, 28 species (72%) were significantly aggregated (Chi Squared test, using 2.5% significance levels). Rice and Lambshead tentatively concluded that analysis of the patch dynamics of nematode populations might be developed as "a general monitoring method for [disturbance assessment in] the deep sea".

A further informative manipulation of the Chi Squared analysis can be performed (Jumars, 1975; Thistle 1978; Jumars and Eckman, 1983; Rice and Lambshead, in press). Briefly, all the species can be treated as replicates and their Chi-Squares added together to obtain a "total Chi-Squared". The total Chi-Squared indicates whether species on the average depart from Poisson distributions in per-core abundances. The Chi-Squared for the nematode species pooled together into "nematodes per core" can be calculated. The "pooled Chi-Squared" indicates whether the per-core abundances of the individual species summed by core produce a Poisson distribution. They will do this if each individual species' abundances are independent and individually Poisson distributed. The pooled Chi-Squared is subtracted from the total Chi-Squared to give the Heterogeneity Chi-Squared. This tests whether the total number of individuals per sample is essentially constant indicating whether the individual species tend to aggregate in the replicates at random, or in concordance (i.e. tendency to agree where to aggregate) or in discordance (i.e. tendency to disagree where to aggregate).

The second method tested here was devised by Warwick and Clarke (in press) who investigated the variability of several shallow water sites with respect to contamination: meiobenthos in organically enriched mesocosms; macrobenthos around oilfields in the North sea; reef corals following the 1982-3 El Nino; and fish on coral reefs in the Maldive islands subjected to mining. Warwick and Clarke use a variant of Taylor's power law where $\log(1 + \text{variance})$ is plotted against $\log(1 + \text{mean})$ for each species in a community and a regression line is fitted through these points. Warwick and Clarke concluded that the slope of the regression line for a community was greater when it was subject to disturbance, i.e. the degree of aggregation against abundance increases from reference to disturbed sites.

There are two potential problems with this method, one theoretical and the other methodological. The theoretical problem is that it is not clear whether single species data conforms to a straight line. There are other possibilities such as quadratic functions, augmented Poisson or negative binomials (Gaston, pers. com.) so it is equally unclear whether multi-species data should theoretically conform to a straight line either. A problem could arise if the variance-mean relationship was non-linear and data sets which were considerably different in abundances were compared. This is discussed by McArdle *et al.* (1990), who demonstrate the problems in making between-species comparisons. The same arguments may apply to between-communities comparisons. But Warwick and Clarke show on empirical grounds that the fit to their data is good. So over the range of values likely to be used in practice the theoretical problem of non-linearity is probably unimportant.

The methodological problem is that Warwick and Clarke included low-abundance species in the data sets analysed, as well as species completely absent from at least one site. Where the number of species in one set of samples is much less than another and the samples are more heavily dominated by a few species (as often happens in contamination situations), the multiple points with zero-mean and zero-variance for absent species and the species with low abundance can have a hugely disproportionate influence on the regression line, anchoring it to the origin and turning the method into a test for relative species richness.

In this paper we repeat Rice and Lambshead's (in press) analysis. The abundance below which species are excluded in this paper is a slightly less conservative "cut-level", than that used previously. Species with mean abundance of 0.50 or less per core are rejected as this is at the lower limit where deviations from randomness can be detected. Warwick and Clarke's method is also repeated using the same cut level to avoid artefacts associated with low abundances.

RESULTS

Plots of variance against mean are shown for the five data sets in Fig. 1. This data confirms Warwick and Clarke's (in press) view that the data is reasonably linear so fitting regression lines are sensible. Table I shows the results of the Chi Squared analysis showing whether nematodes had aggregated, random or regular distributions. Many species were present in too low an abundance to be tested. All species tested were either aggregated or randomly distributed except a single species at SDT that was regularly distributed. This solitary result is probably a statistical artefact (with multiple testing some results will be significant by chance). Table I also shows the percentage of species that fit into the aggregated and random groups. SDT and PAP showed more species aggregating than the undisturbed MAP. The unpolluted shallow station, EB, also showed many species aggregating but the polluted station, AB, showed fewer species that were significantly aggregated. The data sets were tested for aggregation versus random distributions using the reference site, MAP. A two sample Chi-Squared test was employed using Yates' correction for one degree of freedom. PAP was significantly different from MAP ($p < 0.05$) but SDT was not ($p > 0.10$). MAP was also significantly different from the unpolluted EB ($p < 0.01$) but not the polluted AB ($P > 0.10$). If the results for the two shallow sites are compared using the same method then they are also significantly different ($p < 0.01$).

Table II shows the analysis of the heterogeneity Chi-Squared test. Apart from the most undisturbed station (MAP), nematode species tend to be significantly discordant (i.e. species significantly tend to avoid aggregating in the same places). Table III shows the slopes and intercepts of the regression lines for graphs (Fig. 1) of the $\log(\text{variance})$ plotted against the $\log(\text{mean})$. The regression lines for SDT, PAP, EB and AB were tested against the line for MAP for statistical differences

Table I. - Numbers of species significantly aggregated, significantly regular and neither of the above (random), in five benthic nematode communities, with the percentage of the species tested which were aggregated. Abbreviations of site names: MAP - Madeira Abyssal Plain (undisturbed deep sea); SDT - San Diego Trough (biogenic disturbance in deep sea); PAP - Porcupine Abyssal Plain (highly seasonal detritus input in deep sea); EB - Ettrick Bay (unpolluted shallow water); AB - Ayr Bay (polluted shallow water).

	signif. site aggregated	neither	signif. regular	insufficient data	percentage aggregated
MAP	8	30	0	34	21
SDT	21	40	1	54	34
PAP	31	27	0	67	53
EB	41	25	0	27	62
AB	12	26	0	19	32

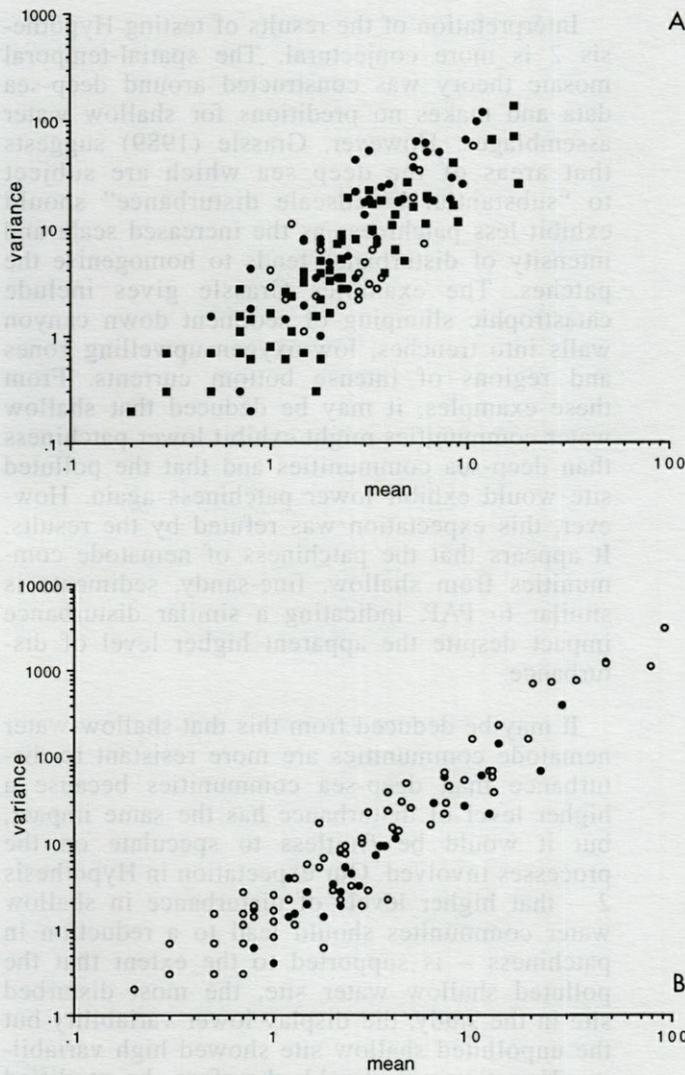


Fig. 1. - Logarithmic plot of variance versus mean abundances of marine nematode species from matched samples. A, Deep sea samples : empty circles - Madeira Abyssal Plain (undisturbed); filled circles - Porcupine Abyssal Plain (highly seasonal detritus input); filled squares - San Diego Trough (biogenic disturbance). B, Shallow water samples : empty circles - Ettrick Bay (unpolluted); filled circles - Ayr Bay (polluted). Parameters of regression lines for this data and their statistical significance are presented in Table III.

Table II. - Comparison of patchiness in total nematode population, individual species independently and individual species as a community, as measured by the "Total Chi Squared", "Pooled Chi Squared" and "Heterogeneity Chi Squared" respectively (Jumars and Eckman 1983). Abbreviations of site names : MAP - Madeira Abyssal Plain (undisturbed deep sea); SDT - San Diego Trough (biogenic disturbance in deep sea); PAP - Porcupine Abyssal Plain (highly seasonal detritus input in deep sea); EB - Ettrick Bay (unpolluted shallow water); AB - Ayr Bay (polluted shallow water). Abbreviations of distribution statistics : A - aggregated; R - randomly aggregated; D - discordantly aggregated; * - P < 0.05; ** - P < 0.01; *** - P < 0.001.

site	total Chi Squared	pooled Chi Squared	heterogeneity Chi Squared
MAP	A***	A***	R
SDT	A***	A***	D***
PAP	A***	A***	D**
EB	A***	A***	D***
AB	A***	A***	D***

Table III. - Comparison of slopes and intercepts of regression lines for logarithmic plots of mean versus variance for five benthic nematode communities. Values with the same letter as superscript are not significantly different at P < 0.05. Abbreviations of site names : MAP - Madeira Abyssal Plain (undisturbed deep sea); SDT - San Diego Trough (biogenic disturbance in deep sea); PAP - Porcupine Abyssal Plain (highly seasonal detritus input in deep sea); EB - Ettrick Bay (unpolluted shallow water); AB - Ayr Bay (polluted shallow water). Abbreviations of distribution statistics : A - aggregated; R - randomly distributed; * - P < 0.05; ** - P < 0.01; *** - P < 0.001.

site	intercept	slope
MAP	0.11 ^A	1.45 [*]
SDT	0.23 ^A	1.41 [*]
PAP	0.56 ^B	1.63 [*]
EB	0.49 ^B	1.63 [*]
AB	0.25 ^A	1.49 [*]

in slope and intercept. There were no significant differences for slope for any of the lines. However, PAP and EB showed significantly higher intercepts, as might be expected from Table I.

DISCUSSION

The lack of any significant differences between the slopes of the regression lines of log (variance) plotted against log (mean) lead us to reject Hypothesis 3. There is no evidence that disturbance changes the rate of aggregation with abundance for marine nematode communities and so this approach should be regarded with caution as a test for pollution induced disturbance. This result was unexpected because the disturbances tested here were resource linked. SDT and PAP have higher organic enrichment than MAP. Both shallow sites are more enriched than the deep-sea sites and AB, in particular, is subject to sewage pollution. Resource-linked disturbances might be expected to increase the rate of aggregation plotted against abundance provided that it is the resource that is driving the aggregation. "The more resources there are, the higher the abundance and the more clumped the animals around the patchy resources" Lamshead and Rice (*in press*). It is not clear why this postulated change in the tendency to aggregate could not be detected but it may be because of the discordancy shown by all the nematode communities affected by disturbance. If species tend to avoid aggregating in the same patches then the species are responding differently to environmental stimuli. So a disturbance event might cause different species to respond in different ways, some species aggregating more and some aggregating less, leaving the community unaltered as a whole. Hence, a regression line will be unaltered.

The analyses seem to support Hypothesis 1. Both methods of analysis show significantly more species aggregated at PAP than MAP. This hypothesis is drawn from Grassle and Morse-Porteous (1987), who suggested that high species richness in the deep-sea benthos (and possibly tropical rainforests) was the result of small scale disturbance acting against a low productivity background over large areas. They suggested that this would produce a mosaic pattern of patchy disequilibria. Grassle (1989) suggested that a disturbance event of increased patchy resources, such as the phytodetritus drop at PAP, might act as a source of patchiness. This process was detected by both the methods of variance analysis tested here. However, the fact that SDT could not be distinguished from MAP suggests that the higher biological activity at SDT did not have the same disturbance impact on the nematode species as the episodic food availability at PAP.

Interpretation of the results of testing Hypothesis 2 is more conjectural. The spatial-temporal mosaic theory was constructed around deep-sea data and makes no predictions for shallow water assemblages. However, Grassle (1989) suggests that areas of the deep sea which are subject to "substantial broadscale disturbance" should exhibit less patchiness as the increased scale and intensity of disturbance tends to homogenise the patches. The examples Grassle gives include catastrophic slumping of sediment down canyon walls into trenches, low-oxygen upwelling zones and regions of intense bottom currents. From these examples, it may be deduced that shallow water communities might exhibit lower patchiness than deep-sea communities and that the polluted site would exhibit lower patchiness again. However, this expectation was refuted by the results. It appears that the patchiness of nematode communities from shallow, fine-sandy, sediments is similar to PAP, indicating a similar disturbance impact despite the apparent higher level of disturbance.

It may be deduced from this that shallow-water nematode communities are more resistant to disturbance than deep-sea communities because a higher level of disturbance has the same impact, but it would be fruitless to speculate on the processes involved. Our expectation in Hypothesis 2 – that higher levels of disturbance in shallow water communities should lead to a reduction in patchiness – is supported to the extent that the polluted shallow water site, the most disturbed site in the study, did display lower variability but the unpolluted shallow site showed high variability. Hypothesis 2 should, therefore, be modified in the light of these results.

Finally, it should be noted that these conclusions rest on only five data sets. The hypotheses need to be tested with more data before methods could be recommended as a reliable way of assessing disturbance. Also, there is a limit to the information that can be gleaned from the examination of replicates of single-sized cores that only examine patchiness at one scale. Multiple-sized corers are required to investigate the processes influencing small-scale patchiness under different disturbance regimes and this is easier in mesocosm experiments than in the field.

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