

# Observations on the use of Taylor's power law to describe the horizontal spatial distribution of marine nematodes in an intertidal estuarine environment

Roy Neilson\*, Brian Boag\* and Christine A. Hackett\*\*

\* Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, Scotland, UK.

\*\* Scottish Agricultural Statistics Service, Invergowrie, Dundee DD2 5DA, Scotland, UK.

Accepted for publication 10 March 1993

**Summary.** The horizontal spatial distributions of marine nematodes at species, genera and family level in an intertidal estuarine environment have been investigated using Taylor's power law index of aggregation  $\beta$ . Different transformations were investigated for their ability to normalise the distributions. Nine of the 15 nematode species; six of the eight genera and five of the six families investigated  $\beta$  had values not significantly different from 2.0. For these a logarithmic transformation would stabilise the variance of the distributions prior to further statistical analysis. The remaining species, genera and families had  $\beta$  values which were significantly less than 2.0. For these a variance-stabilising transformation is given by  $z = x^{1-\beta/2}$ . Some of the detailed information yielded at species and genera level was lost after re-analysing the data at family level.

**Key words:** aggregation, estuarine, marine nematodes, patchiness, spatial distribution, Taylor's power law.

The horizontal distribution of meiofauna, which include marine nematodes as the most abundant taxon, has been shown to be highly variable and aggregated (Coull & Bell, 1979; Heip et al., 1985). Warwick (1988) and Herman & Heip (1988) concluded that meiofauna could be analysed at higher taxonomic levels rather than at species level whilst retaining much of the information. The few studies on the spatial distribution of marine nematodes mostly describe aggregation at the taxa level (Vitiello, 1968; Gray & Rieger, 1971; Arlt, 1973; Olsson & Eriksson, 1974; Findlay, 1981, 1982), with only Gerlach (1977) and Hogue (1982) describing the aggregation of species. They found that nematodes were strongly aggregated on a small spatial scale often around decaying food sources.

Vitiello (1968) and Gerlach (1977) found that the negative binomial distribution described the marine nematode population in their studies. However the negative binomial distribution has severe ecological

limitations (Taylor, 1984; Noe & Campbell, 1985) and Taylor et al. (1979) demonstrated that over a wide range of densities, typical of those found with marine nematodes, the negative binomial aggregation parameter  $k$  could vary with density in a complex way. They concluded that  $k$  was "an unstable parameter whose relationship with aggregation is doubtful" and preferred to use Taylor's variance-mean model (Taylor, 1961) which expresses the variance,  $V$ , as a power of the mean,  $\mu$ , of the distribution:

$$V = \alpha\mu^\beta \quad (1)$$

where  $\beta$  is the index of aggregation and is thought to be constant for individual species (Taylor, 1961) and  $\alpha$  is the "sampling coefficient" (Boag et al., 1987). Taylor's power law (1) does not describe a probability distribution but a relationship between parameters of the distribution. Several theoretical distributions satisfy Taylor's power law (Kemp, 1987). If  $x$  denotes

an observation whose probability distribution satisfies Taylor's power law then the variance is stabilised by the transformation:

$$z = x^{1-\beta/2} \quad (2)$$

(Taylor, 1970; Finch et al., 1975).

Taylor's power law has been used to describe the distribution of terrestrial plant-parasitic nematodes (Boag & Topham, 1985; Ferris, 1985; McSorley et al., 1985; Boag et al., 1987), terrestrial cyst nematodes (Perry, 1983) and gastro-intestinal nematodes of sheep (Boag et al., 1989; Boag et al., 1992) but not marine nematodes.

The purpose of the present paper is (a) to describe the variance-mean relationship of various marine nematode species along a horizontal transect using Taylor's power law, over the range of population sizes which are typically met during ecological studies; (b) to suggest the optimum transformation for stabilising the variance in the data for future statistical analysis; and (c) to determine whether there is any loss of information when the data is re-analysed at higher taxonomic levels.

## MATERIALS AND METHODS

Samples were taken from around a short-fall sewage outlet in Invergowrie Bay (Latitude 56° 27' N, Longitude 3° 03' W), an intertidal area of the Tay Estuary, Scotland (Fig. 1). A total of 60 sediment samples were taken on 16 July 1989 from two transects radiating out in a North West and a South East direction from the mouth of the sewage outlet. Along each transect three replicate samples were collected at each of 10 sampling stations located at 25 m intervals to 175 m and at 225, 275 and 325 m respectively from the sewage outfall.

Sediment samples consisted of cores taken by a corer of 5 cm internal diameter (Boag & Brown, 1985) to a depth of 5 cm. The corer has a tapered rim to minimise boundary compression of the sample when inserted gently into the sediment. Samples were immediately placed in thick gauge polythene bags, to

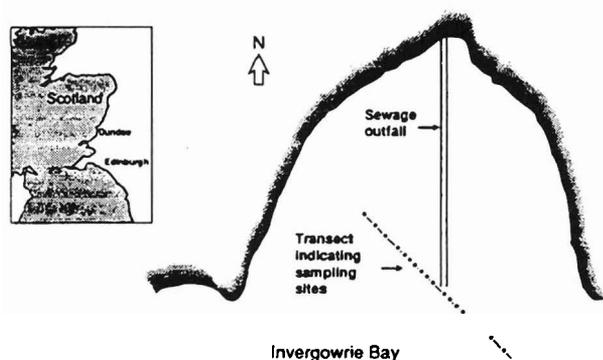


Fig. 1. Schematic map showing location of study area.

which 4% formalin was added. On return to the laboratory, the samples were transferred to glass jars and more 4% formalin was added.

Nematodes were extracted using a flotation technique, a modification of the method described by Warwick et al. (1990). Samples were placed in one litre measuring cylinders, the volume made up to one litre with tap water which had previously been filtered to remove potential contamination by fresh water meiofauna. The cylinders were stoppered and shaken in order to homogenise the sample. Immediately, two 10 ml aliquots were removed using a wide-mouthed pipette and placed into a 100 ml glass beaker. The volume was made up to 50 ml with the addition of 30 ml of Ludox colloidal silica diluted to a final specific gravity of 1.15 and a few drops of Rose Bengal stain, stirred and left for 60 minutes to allow the sediment to settle. The supernatant was decanted on to a 53  $\mu$ m sieve and the extraction repeated. Any nematodes collected on the sieve were washed off using filtered tap water into a glass collecting tube. Nematodes were counted under a low power binocular microscope and approximately the first 200 nematodes encountered were hand-picked and placed into a solution of 1.5% glycerol in distilled water and transferred to 100% glycerol as described by Hooper (1986), before mounting on glass slides for identification. Where possible, identification was to species level using the pictorial keys of Platt & Warwick (1983, 1988, 1993). Where specimens were juveniles, they were identified to genus and divided proportionally between the

identified species within that genus.

Taylor's power law was used to model aggregation for species, genera and families. It postulates a relationship between the mean,  $\mu_i$  and the variance,  $V_i$ , of counts of a species or genus or family on occasion  $i$ :

$$V_i = \alpha \mu_i^\beta \quad (3)$$

where  $\beta$  is the index of aggregation. Taylor proposed that  $\beta$  could be estimated by the regression coefficient of log (variance) on log (mean), i.e.  $\beta$  is estimated by  $b$  where:

$$\log (s_i^2) = a + b \log (m_i) + E_i \quad (4)$$

and where  $m_i$  and  $s_i^2$  are the sample mean and sample variance respectively. Model (4) differs from the normal regression model, since  $\log (m_i)$ , the independent variable, is subject to error with the consequence that the usual least squares estimator,  $b$ , may be an underestimate of  $\beta$ . However, Perry (1981) has discussed a simple method for obtaining an upper bound  $b'$  for  $\beta$  and discussed other assumptions underlying the estimation of  $\beta$  by  $b$ , proposing graphical checks to detect severe violations of these assumptions.

A preliminary examination of the data from each site showed that the second sample consistently had nematode counts at least twice as high as the other two samples; this was thought to be due to two different consignments of Ludox HS30 used to extract the nematodes. Hence the second sample was excluded for the analysis and the data from two adjacent sites were combined to give four replicates from which the mean and variance were calculated (unless all four counts were zero). This will have the effect of slightly underestimating the variance between sites and overestimating the variance at a single site, but is preferable to estimating means and variances from the two remaining replicates at a single site.  $\beta$  was estimated for each taxonomic category according to the regression equation (4) of log (variance + 1) on log (mean + 1) and the validity of the assumptions was

examined.

Different transformations of the data for each species, genus or family were investigated for their ability to normalise the distribution. A plot of the transformed data against the normal order statistics is a straight line with a very high correlation coefficient if the data is normally distributed. This is known as the probability plot correlation test (Filliben, 1975). For the sample sizes used here the hypothesis of normality is rejected if the correlation test statistic is less than 0.972, however, simulations suggest that the critical level of the test should be increased from 0.972 to 0.975.

The statistical program Genstat 5 Release 1.2 (Payne et al., 1987) was used for all calculations.

## RESULTS

The sediment from the study site is a muddy sand with mean particle diameter in the range 134  $\mu\text{m}$  to 175  $\mu\text{m}$ .

The range of  $b$  values for the 15 most common marine nematode species in this study are presented in Table 1. Figure 2 graphically illustrates three species with differing degrees of aggregation. Also in the table are the values of the upper bound,  $b'$ , on the true value of the index, calculated according to Perry (1981) and values for  $a$ , the "sampling coefficient" (Boag et al., 1987). *Anoplostoma viviparum*, *Calomicrolaimus honestus*, *Chromadorita tentabunda*, *Desmolaimus zeelandicus*, *Leptolaimus papilliger* and *Paracanthonus caecus* were strongly aggregated with  $b$  values in the range 1.90 to 2.25, whereas other nematode species were less aggregated with  $b$  values of less than 1.60. *Daptonema* sp. A had a random (Poisson) distribution with a  $b$  value of 0.98. Table 2 indicates that at the generic level *Anoplostoma*, *Leptolaimus*, *Desmolaimus* and *Chromadorita* have  $b$  values between 1.83 and 2.06. However, the  $b$  value for *Daptonema* was 1.11 suggesting a random distribution. The  $b$  value for each species was not significantly different from the  $b$  value for their corresponding genus. Table 2 also shows that all families with the exception of Xyalidae have an

aggregated distribution with values for  $b$  between 1.65 and 3.00.

When the upper bound,  $b'$ , is only slightly higher than  $b$  then  $b$  is a satisfactory estimate of  $\beta$ . However, the species *Desmolaimus zeelandicus* and *Leptolaimus papilliger*, genera *Daptonema* and *Dichromadora* and families Xyalidae and Linhomoeidae have  $b'$  values considerably larger than  $b$ . This may be due to their having few samples with small means and small variances and the remaining samples having larger means, and a wide range of variances. The sampling coefficient  $a$  for the nematodes varied considerably but was generally positive when the  $b$  value was low and negative when the  $b$  value was high.

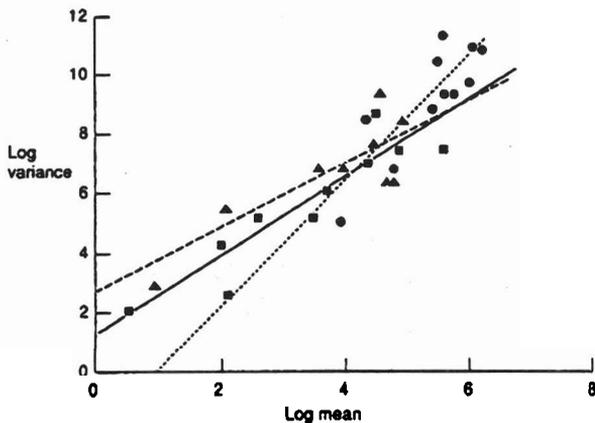


Fig. 2. Plots of log (variance) against log (mean) and fitted regression lines for *Anoplostoma viviparum* (closed circles and short dashed line); *Chromadorina* sp. A (closed squares and solid line) and *Daptonema* sp. A (closed triangles and long dashed line).

Different transformations of the data were compared using the probability plot correlation test (Filliben, 1975) on the residuals after an analysis of variance of the transformed data for station effects. The correlation test statistics are presented in Tables 3 and 4. For 14 of the 15 species the data was approximately normally distributed after a square root transformation. For the cube root transformation and the transformation suggested by Taylor's power law 12 out of 15 species were approximately normally distributed. The hypothesis of normality of the untransformed data and the logarithmically

transformed data was rejected for 10 and 11 species respectively. The transformations were ranked according to the correlation test statistics for each species and a mean rank calculated: this suggested

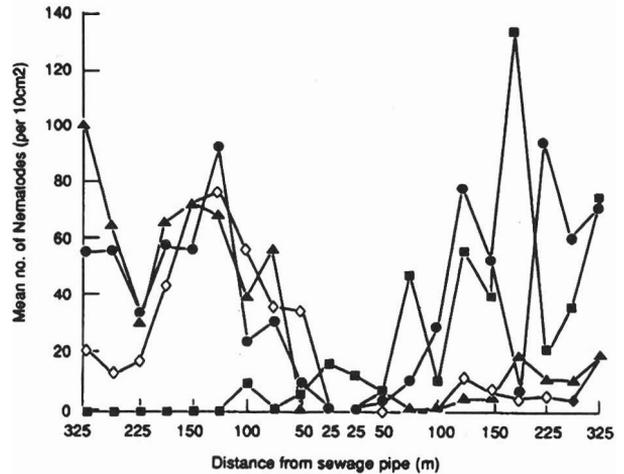


Fig. 3. Mean abundances of the four most prevalent species within the family Xyalidae ( $\Delta$  - *Daptonema tenuispiculum*;  $\bullet$  - *Daptonema* sp. A;  $\diamond$  - *Daptonema procerum*;  $\blacksquare$  - *Daptonema setosum*).

that the best overall transformation was the cube root, followed by the transformation from Taylor's power law. However, the transformation derived from Taylor's power law was rejected for *Calomicrolaimus honestus* and *Chromadorita tentabunda*. This was probably due to the fact that for these two species there were no significant differences between the stations but a large variation within the stations. If the rank scores for these two species were omitted then the best overall transformation would be that suggested from Taylor's power law which agrees with the result for genera and families (Table 4). At the genus and family level, all transformations except the logarithmic and untransformed data normalised the data adequately. The transformation derived from Taylor's power law was frequently the best for both genera and families.

## DISCUSSION

Taylor's power law has been successfully applied to a range of organisms including annelids, molluscs, insects, fish, birds, foxes and men (Taylor et al., 1978; Taylor et al., 1980; Rhodes & Morse, 1989)

Table 1. Estimates of Taylor's power law index of aggregation  $\beta$  for various marine nematode species.

Species	No. of site at which species were present	$b$	Standard error	$a$	Standard error	$b^*$
<i>Anoplostoma viviparum</i>	39	2.06	0.45	-2.02	2.50	2.85
<i>Calomicrolaimus honestus</i>	25	2.09	0.42	-0.57	1.25	2.60
<i>Chromadorina sp. A</i>	33	1.36	0.23	1.30	0.83	1.66
<i>Chromadorita tentabunda</i>	37	2.25	0.40	-1.65	1.82	2.82
<i>Daptonema procerum</i>	22	1.49	0.30	1.61	1.08	1.85
<i>D. setosum</i>	21	1.39	0.26	2.18	1.02	1.64
<i>D. tenuispiculum</i>	25	1.28	0.15	1.99	0.56	1.38
<i>Daptonema sp. A</i>	34	0.98	0.27	2.79	1.10	1.57
<i>Desmolaimus zeelandicus</i>	39	1.91	0.61	-1.21	3.73	3.47
<i>Dichromadora cephalata</i>	35	1.57	0.32	0.91	1.32	2.10
<i>D. geophila</i>	34	1.55	0.25	0.89	0.85	1.87
<i>Leptolaimus papilliger</i>	39	1.90	0.53	-1.56	3.22	3.06
<i>Paracanthonchus caecus</i>	36	1.95	0.42	-0.56	1.90	2.49
<i>Paracantonchus sp. A</i>	23	1.45	0.19	1.71	0.64	1.63
<i>Ptycholaimellus ponticus</i>	24	1.28	0.18	2.19	0.73	1.46

\*  $b^*$  is the upper bound on the true value of the index of aggregation (Perry, 1981).

Table 2. Estimates of Taylor's power law index of aggregation  $\beta$  for different marine nematode genera and families.

	No. of sites at which species were present	$b$	Standard error	$a$	Standard error	$b^*$	No. of contributing species
<b>Genus</b>							
<i>Anoplostoma</i>	39	2.06	0.45	-2.02	2.50	2.85	1
<i>Chromadorina</i>	33	1.36	0.23	1.30	0.83	1.66	1
<i>Chromadorita</i>	39	1.83	0.36	-0.20	1.74	2.40	4
<i>Daptonema</i>	39	1.11	0.53	2.21	2.89	3.13	9
<i>Desmolaimus</i>	39	1.91	0.61	-1.21	3.73	3.47	1
<i>Dichromadora</i>	39	1.64	0.72	0.27	3.74	4.15	4
<i>Leptolaimus</i>	39	2.01	0.49	-2.23	3.04	2.98	2
<i>Paracanthonchus</i>	38	1.65	0.32	0.45	1.52	2.16	3
<b>Family</b>							
<i>Anoplostomatidae</i>	39	2.06	0.45	-2.02	2.50	2.85	1
<i>Chromadoridae</i>	39	3.00	0.52	-8.35	3.18	3.72	14
<i>Cyatholaimidae</i>	38	1.65	0.32	0.45	1.52	2.16	3
<i>Leptolaimidae</i>	39	1.94	0.48	-1.73	2.96	2.89	3
<i>Linchomoeidae</i>	39	1.93	0.60	-1.37	3.70	3.44	3
<i>Xyalidae</i>	39	0.86	0.72	3.88	4.10	5.65	15

\*  $b^*$  is the upper bound on the true value of the index of aggregation (Perry, 1981).

Table 3. Correlation test statistics for a range of transformations of the most prevalent nematode species. (95% significance level = 0.972, Filliben, 1975).

Species	Untrans- formed	V (equivalent b value = 1)	$\sqrt[3]{V}$ (equivalent b value = 1.33)	VV (equivalent b value = 1.5)	$\log(x+1)$ (equivalent b value = 2)	Taylor	b value
<i>Anoplostoma viviparum</i>	0.964	0.980	0.986	0.986	0.984	0.985	2.06
<i>Calomicrolaimus honestus</i>	0.915	0.973	0.956	0.933	0.875	0.863	2.09
<i>Chromadorina sp. A</i>	0.978	0.988	0.991	0.973	0.883	0.991	1.36
<i>Chromadorita tentabunda</i>	0.993	0.997	0.998	0.998	0.888	0.802	2.25
<i>Daptonema procerum</i>	0.940	0.975	0.976	0.971	0.939	0.974	1.49
<i>D. setosum</i>	0.955	0.966	0.960	0.942	0.876	0.959	1.39
<i>D. tenuispiculum</i>	0.971	0.982	0.976	0.960	0.903	0.977	1.28
<i>Daptonema sp. A</i>	0.962	0.988	0.968	0.925	0.793	0.988	0.98
<i>Desmolaimus zeelandicus</i>	0.966	0.983	0.989	0.991	0.995	0.995	1.91
<i>Dichromadora cephalata</i>	0.985	0.988	0.992	0.988	0.916	0.990	1.57
<i>D. geophila</i>	0.984	0.984	0.992	0.982	0.893	0.987	1.55
<i>Leptolaimus papilliger</i>	0.992	0.988	0.988	0.989	0.993	0.992	1.90
<i>Paracanthochus caecus</i>	0.938	0.978	0.987	0.990	0.991	0.992	1.95
<i>Paracanthochus sp. A</i>	0.969	0.991	0.990	0.989	0.951	0.992	1.45
<i>Ptycholaimellus ponticus</i>	0.908	0.980	0.981	0.952	0.827	0.980	1.28
No. of acceptances	5	14(13)	12	9(8)	4	12(11)	
No. of rejections	10	1(2)	3	6(7)	11	3(4)	
No. of optimum transformations	-	4	7	1	2	5	
Rank* (1 = best overall trans- formation, 6 = poorest overall transformation)	5	3	1	4	6	2	

\*Rank calculated by awarding a score of one for optimum transformation, two for next best transformation etc and summing across species. Figures in parentheses indicate the number of acceptances or rejections using the 95% significance level of 0.975 derived from simulated data.

suggesting that it is robust and can describe aggregation over a wide range of population densities and conditions.

Taylor (1971) suggested that the degree of aggregation could be a characteristic of a particular species since it resulted from the unique interactions between that species and its environment. Several environmental processes have been suggested as being capable of generating aggregations of meiobenthos, including attraction to food (Gerlach, 1977; Lee et al. 1977; Olafsson, 1992); association with biogenic sediment structures (Bell et al., 1978; Findlay, 1981); sediment microtopography (Hogue & Miller, 1981) and intraspecific competition (Heip, 1975). Although it is not within the scope of this study to determine the reasons for marine nematode spatial

distribution, there appeared to be either possible interspecific competition within the family Xyalidae for the available food resources and or the observed pattern could result from the species having different micro-habitat preferences. Figure 3 shows the abundances of the four more prevalent species within Xyalidae, indicating that *Daptonema setosum* rarely co-exists with either *D. tenuispiculum* or *D. procerum*, however, *D. tenuispiculum* and *D. procerum* seem to co-exist with each other. Interspecific faunal affinities will be dealt with more thoroughly in a future publication.

The results confirm that some species have different degrees of aggregation e.g. *A. viviparum* is highly aggregated whereas *Chromadorina sp. A* is significantly less aggregated and *Daptonema sp. A*

Table 4. Correlation test statistics for a range of transformations of the most prevalent nematode genera and families (95% significance level = 0.972, Filliben, 1975).

Species	Untransformed	$\sqrt{y}$ (equivalent b value = 1)	$\sqrt[3]{y}$ (equivalent b value = 1.33)	$\sqrt{y^2}$ (equivalent b value = 1.5)	$\log(x+1)$ (equivalent b value = 2)	Taylor	b value
<b>Genus</b>							
1. <i>Anoplostoma</i>	0.964	0.980	0.986	0.986	0.984	0.985	2.06
2. <i>Chromadorina</i>	0.978	0.988	0.991	0.973	0.883	0.991	1.36
3. <i>Chromadorita</i>	0.971	0.990	0.992	0.993	0.996	0.996	1.83
4. <i>Daptonema</i>	0.992	0.996	0.995	0.994	0.987	0.996	1.11
5. <i>Desmolaimus</i>	0.966	0.983	0.989	0.991	0.995	0.995	1.91
6. <i>Dichromadora</i>	0.996	0.991	0.990	0.988	0.987	0.987	1.64
7. <i>Leptolaimus</i>	0.995	0.991	0.989	0.989	0.993	0.993	2.01
8. <i>Paracanthonus</i>	0.981	0.989	0.986	0.985	0.980	0.983	1.65
No. of acceptances	5	8	8	8(7)	7	8	
No. of rejections	3	-	-	-(1)	1	-	
No. of optimum transformation	2	2	2	1	2	4	
Rank* (1 = best overall transformation, 6 = poorest overall transformation)	6	3	2	4	5	1	
<b>Family</b>							
Anoplostomatidae (1)	0.964	0.980	0.986	0.986	0.984	0.985	2.06
Chromadoridae (2, 3, 6)	0.989	0.986	0.985	0.985	0.987	0.994	3.00
Cyatholaimidae (8)	0.981	0.989	0.986	0.985	0.980	0.983	1.65
Leptolaimidae (7)	0.993	0.993	0.994	0.995	0.996	0.996	1.94
Linhomoeidae (5)	0.995	0.988	0.988	0.987	0.986	0.987	1.93
Xyalidae (4)	0.994	0.997	0.997	0.995	0.988	0.997	0.86
No. of acceptances	5	6	6	6	6	6	
No. of rejections	1	-	-	-	-	-	
No. of optimum transformation	1	2	2	1	1	3	
Rank* (1 = best overall transformation, 6 = poorest overall transformation)	5	3	2	4	6	1	

\*Rank calculated by awarding a score of one for optimum transformation, two for next best transformation etc and summing across species. Figures in parentheses after family names indicate which genus belongs to that family.

Figures in parentheses indicate the number of acceptances or rejections using the 95% significance level of 0.975 derived from simulated data.

has a random distribution. This study has also shown that similarity exists between species within the same genus e.g. *Dichromadora cephalata* and *D. geophila* have *b* values of 1.57 and 1.55 respectively. Similarly species within the genus *Daptonema*, namely *D. procerum*, *D. setosum*, *D. tenuispiculum* and *Daptonema* sp. A have *b* values of 1.49, 1.39, 1.28 and 0.98 respectively which are not significantly different.

Estimating  $\beta$  at the generic level would appear to retain most of the information yielded at the species level. However, that detailed information is lost when

analysing families with a large number of species e.g. Chromadoridae whose horizontal spatial distribution is deemed to be more highly aggregated. This has implications for future studies on horizontal spatial distribution of marine nematodes as a decision on which taxonomic level to study must be carefully considered.

Field et al. (1982) and Clarke & Green (1988) suggested that either the logarithmic or the double square root transformation should be used to stabilise variance in sets of marine benthic data prior to

statistical analysis. These transformations were used on the complete data set, ignoring the possibility of different distributions among species. For nine out of the 15 most prevalent nematode species in our present study, the  $b$  value did not differ significantly from 2.0. This value of  $b$  corresponds to a logarithmic transformation. However, six of the species investigated had  $b$  values significantly less than 2.0 e.g. *Daptonema tenuispiculum* with  $b=1.28$ . The data may be transformed using equation (2) allowing further analysis such as analysis of variance, regression or community structure analysis to be carried out on the transformed scale. From the results of this study it appears that the double square root and the logarithmic transformations are inappropriate for transforming our complete data set, ranking only fourth and sixth respectively, whereas, an overall cube root transformation would be an acceptable compromise. However, we suggest transforming the most prevalent species on an individual basis and then transforming the less prevalent species as one using Taylor's power law.

It would be interesting to determine whether the same values as would be obtained in a different environment as suggested by Taylor (1971). Unfortunately, to our knowledge there is a general lack of appropriate published data sets on marine nematodes with a sufficient number of samples to allow this hypothesis to be tested from other marine biotopes e.g. a sandy, sublittoral environment or similar biotopes from different geographic regions.

## ACKNOWLEDGEMENTS

We thank Dr T.J. Ferrero of the British Museum (Natural History), London for confirming the identification of some of the marine nematode species; Drs D.J.F. Brown and A. Jones for useful discussions; Mr J.W. McNicol for his critical reading of the manuscript; Lisa Palmer for technical assistance, the Scottish Crop Research Institute and the Scottish Office Agriculture and Fisheries Department for funding to allow one of us (RN) to carry out this work towards a higher degree.

## REFERENCES

- Arlt, G. 1973. Vertical and horizontal microdistribution of the meiofauna in the Greifswalder Bodden. *Oikos*, Supplement 15: 105-111.
- Bell, S. S., Watzin, M. C. & Coull, B. C. 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. *Journal of Experimental Marine Biology and Ecology* 35: 99-107.
- Boag, B. & Topham, P. B. 1985. Aggregation of plant parasitic nematodes and Taylor's power law. *Nematologica* 30: 348-357.
- Boag, B. & Brown, D. J. F. 1985. Soil sampling for virus-vector nematodes. *Aspects of Applied Biology* 10: 183-189.
- Boag, B., Brown, D. J. F. & Topham, P. B. 1987. Vertical and horizontal distribution of virus vector nematodes and implications for sampling procedures. *Nematologica* 33: 83-96.
- Boag, B., Topham, P. B. & Webster, R. 1989. Spatial distribution on pasture of infective larvae of the gastro-intestinal nematode parasites of sheep. *International Journal of Parasitology* 19: 681-685.
- Boag, B., Hackett, C. A. & Topham, C. A. 1992. The use of Taylor's power law to describe the aggregated distribution of gastro-intestinal nematodes of sheep. *International Journal of Parasitology* 22: 267-270.
- Clarke, K. R. & Green, R. H. 1988. Statistical design and analysis for a 'biological effects' study. *Marine Ecology; Progress Series* 46: 213-226.
- Coull, B. C. & Bell, S. S. 1979. Perspectives of marine meiofauna ecology. In: *Ecological Processes in Coastal and Marine Systems*. (R.J. Livingston. Ed.) pp. 189-216. New York, Plenum Press.
- Ferris, H. 1985. Population assessment and management strategies for plant-parasitic nematodes. *Agriculture, Ecosystems and Environment* 12: 285-299.
- Field, J. G., Clarke, K. R. & Warwick, R. M. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology; Progress Series* 8: 37-52.
- Filliben, J. R., 1975. The probability plot correlation coefficient test for normality. *Technometrics* 17: 111-117.
- Finch, S., Skinner, G & Freeman, G. H. 1975. The distribution and analysis of cabbage rootfly egg populations. *Annals of Applied Biology* 79: 1-18.
- Findlay, S. E. G. 1981. Small-scale spatial distribution of meiofauna on a mud- and sandflat. *Estuarine, Coastal, and Shelf Science* 12: 471-484.
- Findlay, S. E. G. 1982. Influence of sampling scale on apparent distribution of meiofauna on a sandflat. *Estuaries* 5: 322-324.
- Gerlach, S. A. 1977. Attraction to decaying organisms as a possible cause for patchy distribution of nematodes in a Bermuda beach. *Ophelia* 16: 151-165.

- Gray, J. S. & Rieger, R. M. 1971. A quantitative study of the meiofauna of an exposed sandy beach, at Robin Hood's Bay, Yorkshire. *Journal. Marine Biological Association* 51: 1-19.
- Heip, C. 1975. On the significance of aggregation in some benthic marine invertebrates. In: *Proceedings of the 9th European Marine Biology Symposium*. (H. Barnes. Ed.) pp. 527-538. Aberdeen University Press.
- Heip, C., Vincx M. & Vranken, G. 1985. The ecology of marine nematodes. *Oceanography and Marine Biology. An Annual Review* 23: 399-489.
- Herman, P. M. J. & Heip, C. 1988. On the use of meiofauna in ecological monitoring: who needs taxonomy? *Marine Pollution Bulletin* 19: 665-668.
- Hogue, E. W. & Miller C. B. 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology* 52: 181-191.
- Hogue, E. W. 1982. Sediment disturbance and the spatial distributions of shallow water meiobenthic nematodes on the open Oregon coast. *Journal of Marine Research* 40: 551-573.
- Hooper, D. J. 1986. Handling, fixing, staining and mounting nematodes. In: *Laboratory Methods for Work with Plant and Soil Nematodes*. (J.F. Southey. Ed.) pp. 59-80, HMSO, London.
- Kemp, A. W. 1987. Families of discrete distributions satisfying Taylor's power law. *Biometrics* 43: 693-699.
- Lee, J. J., Tietjen, J. H., Mastropaolo, C. & Rubin, H. 1977. Food quality and the heterogeneous spatial distribution of meiofauna. *Helgolaender Wissenschaftliche Meeresuntersuchungen* 30: 272-282.
- McSorley, R., Dankers, W. H., Parrado, J. L. & Reynolds, J. S. 1985. Spatial distribution of the nematode community on Perrine Marl soils. *Nematropica* 15: 77-92.
- Noe, J. P. & Campbell, C. L. 1985. Spatial pattern analysis of plant-parasitic nematodes. *Journal of Nematology* 17: 86-93.
- Olafsson, E. 1992. Small-scale spatial distribution of marine meiobenthos: the effects of decaying macrofauna. *Oecologia* 90: 37-42.
- Olsson, I. & Eriksson, B. 1974. Horizontal distribution of meiofauna within a small area, with special reference to foraminifera. *Zoon* 2: 67-84.
- Payne, R. W., Lane, P. W., Ainsky, A. E., Bicknell, K. E., Digby, P. G. N., Harding, S. A., Leech, P. K., Simpson, H. R., Todd, A. D., Verrier, P. J. & White, R. P. 1987. *Genstat 5 Reference Manual*, Clarendon Press, Oxford, pp. 1-749.
- Perry, J. N. 1981. Taylor's power law for dependence of variance on mean in animal populations. *Applied Statistics* 30: 254-263.
- Perry, J. N. 1983. Effects of spatial heterogeneity on Jones' model for cyst-nematodes population dynamics and crop root damage. *Journal of Applied Ecology* 20: 849-856.
- Platt, H. M. & Warwick, R. M. 1983. *Freeliving marine nematodes. Part I. British Enoplids*. (D.M. Kermack & R.S.K. Barnes. Eds.) pp. 1-307. Cambridge University Press, Cambridge, UK.
- Platt, H. M. & Warwick, R. M. 1988. *Freeliving marine nematodes. Part II. British Chromadorids*. (D.M. Kermack & R.S.K. Barnes. Eds.) E.J. Brill, Leiden, Netherlands, pp. 1-502.
- Platt, H. M. & Warwick, R. M. 1993. *Freeliving marine nematodes. Part III. British Monhysterids*. (In preparation).
- Rhodes, A. A. & Morse, J. G. 1989. *Scirtothrips citri* sampling and damage prediction on California Nowel Oranges. *Agriculture, Ecosystems and Environment* 26: 117-129.
- Taylor, L. R. 1961. Aggregation, variance and the mean. *Nature (London)* 189: 732-735.
- Taylor, L. R. 1970. Aggregation and the transformation of counts of *Aphis fabae* Scop. on beans. *Annals of Applied Biology* 65: 181-189.
- Taylor, L. R. 1971. Aggregation as a species characteristic. In: *Statistical Ecology*. Vol. 1, *Spatial Patterns and Statistical Distributions*. (G.P. Patil, E.C. Pielou & W.E. Waters. Eds.) pp. 357-363. The Pennsylvania State University Press, Pennsylvania, USA.
- Taylor, L. R. 1984. Assessing and interpreting the spatial distribution of insect populations. *Annual Review Entomology* 29: 321-357.
- Taylor, L. R., Woiwod I. P. & Perry, J. N. 1978. The density-dependence of spatial behaviour and the rarity of randomness. *Journal of Animal Ecology* 47: 383-406.
- Taylor, L. R., Woiwod I. P. & Perry, J. N. 1979. The negative binomial as an ecological model and the density dependence of  $k$ . *Journal of Animal Ecology* 48: 289-304.
- Taylor, L. R., Woiwod I. P. & Perry, J. N. 1980. Variance and the large scale spatial stability of aphids, moths and birds. *Journal of Animal Ecology* 49: 831-854.
- Vitiello, P. 1968. Variations de la densite du microbenthos sur une aire restreinte. *Recueil des Travaux. Station Marine d'Endoume. Bulletin* 43: 261-270.
- Warwick, R. M. 1988. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin. London* 19: 259-268.
- Warwick, R. M., Platt, H. M., Clarke, K. R., Agard, J. & Gobin, J. 1990. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. *Journal of Experimental Marine Biology and Ecology* 138: 119-142.

**Neilson R., Boag B., Hackett C.A.** Об использовании правила степени Тэйлора для описания горизонтального распределения популяций морских нематод в литорали в зоне эстуария.

**Резюме.** В экосистеме литорали в зоне эстуария исследовали на основе вычисления индекса агрегированности  $\beta$  правила степени Тэйлора горизонтальное распределение видов, родов и семейств морских нематод. Применяли различные способы преобразования данных с целью их оптимальной нормализации. Девять из 15 видов, шесть из восьми родов и пять из шести исследованных семейств имели значение  $\beta$  незначительно отличающееся от 2,0. Для них наилучшим преобразованием перед дальнейшей статистической обработкой было логарифмическое. Остальные виды, роды и семейства имели значение  $\beta$  существенно меньше, чем 2,0. Для них подобная трансформация данных имела вид:  $z = x^{1-\beta/2}$ . Некоторые закономерности, отмеченные на уровне вида и рода информационно терялись при повторном анализе данных на уровне семейства.

---