Ecological Biodiversity of Marine Nematodes in Samples from Temperate, Tropical, and Deep-Sea Regions

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Abstract: *Little is known about the biodiversity of free-living nematodes. We have attempted to provide baseline information about the natural diversities (those not influenced by pollution) that might be expected in six biotopes. Seventeen marine nematode data sets consisting of 197 samples were standardized to allow a comparison of alpha diversity, or sample diversity, from temperate estuarine, tropical sublittoral, temperate sublittoral, bathyal, abyssal, and hadal biotopes, which were selected on criteria of depth and latitude. The diversity analysis methods we employed were rarefaction curves; three weighted diversity indices of species richness, SR, H′, and ES(X); and two equitability indices, J′ and V. Diversity was significantly different in the six biotopes. The weighted indices of species richness were more capable of resolving differences between the biotopes than were the equitability indices, whose large standard errors suggested that they were more influenced by local, small-scale ecological factors. This suggests that species richness is a better measure than equitability for large-scale comparisons of biotopes or regions. The ES(X), which is robust to sample size variations, was more efficient than the weighted indices of species richness, which were easily influenced by sample size. There was a nonlinear relationship between depth and diversity with the bathyal and abyssal biotopes displaying the highest diversity. The tropical sublittoral biotope was not more diverse than the temperate sublittoral biotope. The lowest diversities were found in the physically challenging temperate estuarine and hadal biotopes.*

Biodiversidad ecológica de los nematodes marinos en muestras de regiones templadas, tropicales y de aguas profundas.

Resumen: *Poco se conoce acerca de la biodiversidad de los nemátodos. En este estudio intentamos proveer información básica acerca de las diversidades naturales (es decir no influenciadas por la contaminación) que deberían observarse en seis biotopos. Se estandarizaron 17 grupos de datos de nemátodos marinos, de 197 muestras, para permitir la comparación de la diversidad alfa (diversidad muestral) de los siguientes biotopos, seleccionados en base a criterios de profundidad y latitud: estuarinos templados, sublitoral tropical, sublitoral templado, batial, abisal y hadal. Los Métodos de análisis de diversidad que empleamos fueron curvas de rarefacción, tres índices de riqueza de especies, SR, H′, y ES(X); y dos índices de equitabilidad, J′ y V. La diversidad diferente significativamente entre los seis biótopos . Los índices de riqueza de especies resolvieron mejor las diferencias entre los biotopos que los índices de equitabilidad, cuyos grandes errores estandar sugirieron que son más influenciados por factores ecológicos locales de pequeña escala. Esto sugiere que la riqueza de especies es una mejor medida que la equitabilidad para comparaciones de biótopos o regiones a gran escala. El índice ES(X) que es robusto en cuanto a variaciones en el tamaño de meustra de, fue más eficiente que los índices de riqueza de especies, los cuales son fácilmente influenciados por el tamaño muestral. Existió*

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una relación no linea entre la profundid y la diversidd en los biótopos batial y abisal que exhibieron la mayor diversidad. El biotopo sublitoral tropical fue menos diverso que el biótopo sublitoral templado. Las diversidades más bajas se encontraron en los biotopos estuarinos templado y hadal que son físicamente más exigentes.

Introduction

Nematodes are considered the most abundant metazoan taxon, with estimates that 80% (Bongers 1988) or 90% (Jairajpuri & Ahmad 1992) of all metazoa are nematodes. Recently, it has been claimed that nematodes are one of the three major radiations that have produced most of the world's multicellular species (May 1988; Gaston 1991). Lambshead (1993) estimates that there may be as many as 1×10^8 nematode species in the deep sea, but the number of described species of nematodes is only about 20,000, of which more than 4000 are free-living marine organisms (Gerlach 1980). These figures are low in comparison with the estimated number of insect species described (about 80,000; Gaston 1991), which probably reflects the proportion of nematologists to entomologists.

It is clear that if Lambshead (1993) is even close with his estimate of one hundred million nematode species, then only a tiny portion has been described, most of which are northwest European coastal animals. It is therefore impossible to investigate marine nematode biogeographic distributions. Similarly, it is not possible to pool samples to determine the total number of different species found in a region or area. The vast majority of species in most areas of the world, but especially in the deep sea and tropics, are undescribed, and equitability is high. It would be a major taxonomic initiative involving the examination of hundreds of thousands of specimens to determine conspecificity among similar animals collected over a region, a problem beyond the scope of this paper.

Methods

It is feasible to study the ecological biodiversity of nematodes by sorting worms in samples into nominal species based on their morphology. Marine benthic biologists place greater emphasis on sample diversity than on regional diversity, unlike their colleagues who study terrestrial organisms. In addition to the taxonomic problems alluded to above, this is partly because marine benthic samples are more quantitative than terrestrial samples, which tend to be self-selected, nonrandom, and inefficient (due to, for example, light traps and tree fogging). It is also more difficult for marine biologists, especially deep-sea workers, to define what constitutes a region, given the unitary nature of the world ocean. Terrestrial regions are commonly marked by vegetation type, but this has no direct marine equivalent because most primary production in the seas is carried out by small, floating organisms in the upper water layers.

Marine samples do allow an accurate estimation of alpha diversity, defined as the diversity within a uniform habitat or patch (Heip et al. 1988). This is to some extent a theoretical concept because well-defined patches may not exist in most marine habitats (Jumars 1976; Jumars & Eckman 1983). Recent research on seasonal flux effects on deep-sea meiofauna suggest that in practice a core sample can be treated as a single patch (Lambshead & Gooday 1990; Rice & Lambshead 1992; Lambshead & Hodda 1994).

The main problems experienced by Boucher (1990) in comparing subtidal tropical and temperate samples were with standardization of parameters such as sample size and with methods of analyzing diversity so as to ensure the validity of the comparisons. In this study, we extend the scope of Boucher (1990) to include additional biotopes from the temperate littoral and deep sea. We attempt to overcome some of the standardization problems by recalculating diversity from original data, either our own or data kindly supplied by colleagues.

We test whether there are differences in marine nematode sample (or alpha) diversity between biotopes (not regions). We investigate sample size and core penetration to test whether sampling artifacts severely influence the results. Similarly, we test abundance and sediment type to check whether any putative differences between biotopes are the result of overriding ecological factors. These factors were chosen because they have been regularly reported and have been considered of general importance in the literature.

Nematode Biodiversity and Conservation

Free-living marine nematodes, as a group, are in no immediate danger of extinction. Their biodiversity is so high and their capacity for meeting environmental challenges so robust that they would probably be among the last taxa to disappear even in an environmental catastrophe. Our interest in nematodes, from a biodiversity point of view, rests largely in what we can learn from them about the forces that shape ecological communities. The study of meiofauna communities is relatively new (the term meiofauna was coined by Mare [1942]). For example, only eight published studies have examined the structure of deep-sea nematode communities at the species level (Lambshead 1993; Lambshead et al.

1994). The high species richness and abundance of nematodes allows statistically analyzable, quantitative core samples to be obtained from small, precisely located, subsections of the environment. This, coupled with a short life span, a conservative reproductive strategy (no dispersion phase), and intimate contact with pore water, suggests that nematodes would make effective pollution-impact monitoring organisms (Boucher 1981; Lambshead 1986). Over 200 publications concerning pollution and nematodes and other meiofauna have now been published (Coull & Chandler 1992). The same properties of nematode communities that have made them useful for pollution monitoring have also made them a valuable tool for investigating various processes that determine community biodiversity. For example, theories of the role of patch dynamics in the maintenance of deep-sea biodiversity have been successfully tested using nematodes (Rice & Lambshead 1992; Lambshead & Hodda 1994). Because nematodes are ubiquitous and are commonly found in all marine sedimentary habitats, comparison of the effects of different environmental conditions are possible.

Biologists generally accept that the best way of conserving genetic diversity is to conserve viable species populations, and that the best way to conserve species is to preserve their communities and habitats. Knowledge of the processes that control the maintenance of biodiversity over ecological time scales is critical to achieve this objective, and nematode communities provide a useful natural tool for investigating these processes. We attempt to assemble a data set from a variety of biotopes from around the world to provide baseline information about the natural diversities that might be expected in a number of different biotopes.

Biotopes

There is a long-standing tradition of dividing samples into major groupings, here called biotopes, to compare ecological biodiversity (Sanders 1968). We selected our biotopes according to two criteria, depth and latitude. The selection follows historical precedent, so the biotopes are to some degree arbitrary. The data used came from 17 sites (197 samples) and were fitted into six biotopes: (1) temperate estuarine (**TE**), including both estuarine and fully marine enclosed-sea areas; (2) tropical sublittoral (**T**); (3) temperate sublittoral (**TS**); and three deep-sea biotopes, (4) bathyal (**B**), (5) abyssal (**A**), and (6) hadal (**H**). Polar, southern temperate, and tropical littoral data were not available. In marine biological terminology *littoral* is the tidal zone, *sublittoral* is from the low water mark to 200 m depth (roughly corresponding to the shelf break), *bathyal* from 200 m to 2 km (roughly corresponding to the upper continental slope), *abyssal* from 2 to 6 km (roughly corresponding to the lower slope, continental rise, and abyssal plain proper), and *hadal* more than 6 km (the ultra abyssal region including trenches).

Standardization and Selection of Data

Sampling and processing procedures have caused considerable problems in interpreting results (Sanders 1968; Abele & Walters 1979*a*, 1979*b*). Abele and Walters (1979*a*) define four main criteria for standardization: sampling and processing procedures, sample size, homogeneity of taxonomic composition, and within-habitat sampling. We have used only data from core samples taken either from specialist meiofauna samplers (hand-held shallow-water corers and deep-sea *Alvin* and multiple corers) or from cores inserted by hand into samples taken with box-corers or grabs.

It is not possible to control sample size when reusing data collected for other purposes. Also, it is not clear in benthic research whether it is more appropriate to standardize for number of specimens or area sampled (Gentil & Dauvin 1988). In marine nematology, it is traditional to standardize for number of specimens because the area sampled by a corer is usually considered sufficiently large to obtain a representative sample. Sample size is thus an artificial product of the technique employed by the investigator and, unlike abundance, does not reflect the densities of the organisms in the environment. Some methods for analyzing diversity are notoriously influenced by sample size, so in this analysis sample size (Table 1) is one of the variables analyzed in order to test for its artifactual contribution to sample diversity.

With benthic nematodes there is a further complication in that they are found at different depths in the sediment, depending on ecological conditions. So corer penetration into the sediment (Table 1) is analyzed here for its potential artifactual impact on alpha-diversity.

Homogeneity of taxonomic composition between sites is not an issue, but taxonomic consistency is important for comparing the diversity of samples. This is particularly true for a taxonomically difficult group, such as nematodes, in which many of the species are undescribed "nominal species" (which is why it is nearly impossible to calculate regional species richness). We have as far as possible used our own data and data from colleagues at The Natural History Museum (London) and the Muséum National d'Histoire Naturelle de Paris. Exchange visits were made to study other collections to ensure taxonomic consistency (the HEBBLE collections, curated at Florida State University, were examined by P. J. D. Lambshead. Other data were generously supplied by authors whose taxonomic methodology is, we believe, sufficiently similar to our own. Finally, disparities in the methods utilized for diversity analysis can make it very difficult to compare published results from different authors (Soetaert et al. 1991). We have only used studies for which we have the original data to recalculate all diversity indices to ensure comparability.

The final criteria for standardization laid down by Abele and Walters (1979*a*) represents within-habitat

Table 1. The biotopes, 17 data sets, and environmental parameters grouped as classes.

		*Environmental parameters**					
Biotype	*Site*	*NS*	*SS*	*Dp*	*Sed*	*Pen*	*Ab*
Temperate-Estuarine	Pempoul	7	2	1	S	2	5-6
	Clyde	6	3-4	1	S	2	5-6
	Lynher	4	5	1	M	3	6
Tropical-Sublittoral	Guadeloupe	12	2	2	M-S	2	3-6
	New Caledonia	30	2	3	M-S	2	2-5
	Great Barrier Reef	9	3	3	M-S	3	3-5
Temperate-Sublittoral	Pierre Noire	30	2	3	S	2	2-5
	Banyuls	12	5	3	M	3	5-6
	Irish Sea	15	3	3	M-S	3	5-6
Bathyal	San Diego Trough	6	3	4	M	1	1-2
	Rockall Trough	9	3	4	M	1	2-4
Abyssal	Porcupine Plain	6	1-4	5	M	1	1-3
	Madeira Plain	6	1-3	5	M	1	1-2
	HEBBLE	18	1-3	5	M	1	——
	Puerto Rico	3	2-3	5	M	3	——
	Hatteras Plain	2	3-4	5	M	3	——
	Venezuela Basin	6	3	5	M	3	——
Hadal	Puerto Rico	9	2-3	6	M	3	——
Number of classes		18	5	6	2	3	6

**NS = number of samples in data set; SS = number of nematodes in sample (1 = 1-90, 2 = 91-110, 3 = 111-250, 4 = 251-450, 5 = 451+); Dp = depth of site (1 = littoral, 2 = shallow sublittoral [< 3 m], 3 = sublittoral, 4 = bathyal, 5 = abyssal, 6 = trench); Sed = sediment type (S = sand, M = mud and ooze); Pen = penetration of sampler into sediment (1 = 1 cm, 2 = medium, 3 = whole core); Ab = abundance of nematodes at site, as number per 10 cm^2 (1 = 0-100, 2 = 101-250, 3 = 251-500, 4 = 501-1000, 5 = 1001-5000, 6 = 5001+; —— indicates data unavailable).*

sampling. All the samples should be taken from a similar grain-size sediment from all biotopes; heterogeneity, or patch effects, should be at a similar level in all sediment samples. This criterion cannot be met, so these factors must be tested (Table 1) to determine whether putative diversity differences between biotopes are actually the result of nonrandom distribution of these factors among biotopes. Undoubtedly, there are other important parameters, but these are the ones that summarize ecological processes that influence nematode diversity and for which we can obtain data from the literature.

The impact of small-scale sediment heterogeneity on nematode diversity is only beginning to be investigated (Rice & Lambshead 1992; Lambshead & Hodda 1994) and has been little studied by zoologists (Pianka 1966). Rice and Lambshead (1992), however, suggest that resources are to some degree indicated by densities per area. So nematode abundance at the sample site was used as a crude measure of resources. Sediment grain size is often reported in the literature, at least in broad outline (muds versus sands), and is commonly supposed to influence diversity because sands are higher-diversity sediments than muds (Wieser 1960; Hopper & Meyers 1967; Tietjen 1977, 1980). Therefore, sediment composition is one of the criteria tested here (mud is defined as sediment having more than 15% silt content).

Seventeen data sets met the criteria listed above (Table 1). Most data are from published work, so to save space a redescription of the sites is omitted here. The relevant authorities are as follows: Guadeloupe, Caribbean (Boucher & Gourbault 1990); New Caledonia, south west Pacific (Boucher & Clavier 1990; Clavier et al. 1990); Great Barrier Reef, Australia (Tietjen 1991); Pierre Noire, France, western English Channel (Boucher 1983); Banyuls, France, Mediterranean (de Bovée 1982); Irish Sea (Platt & Ferrero, unpublished data—four sand and one mud sediment stations of Dublin Bay at 39-56 m depth); Pempoul, France, western English Channel (Boucher, unpublished data—collected monthly in medium sand, 1 m above sea level, spring tide chart data from an oyster bed located in the Bay of Morlaix); Clyde inland sea area, Scotland, Atlantic coast (Lambshead 1986); Lynher Estuary, southwest England (Warwick & Price 1979); San Diego Trough, California, and Rockall Trough, Scotland (Lambshead et al. 1994); Porcupine Abyssal Plain and Madeira Abyssal Plain, northeast Atlantic (Lambshead, Ferrero, and Gooday, unpublished data); sites described in Rice and Lambshead (1992); HEBBLE, northwest Atlantic (Thistle & Sherman 1985); Puerto Rico Trench, Caribbean, and Hatteras Abyssal Plain, northwest Atlantic (Tietjen 1989); Venezuela Basin, Caribbean (Tietjen 1984).

As indicated in Table 1, there is a good spread of samples across the six biotopes, with the possible exception of the Hadal biotope. As shown in the table, for the analysis the raw data were blocked into five nematode sample-size classes, six depth classes, two sediment-type classes, three sampler-penetration classes, and six nematode-abundance classes. The classes chosen were to some degree arbitrary. The boundaries and number of

classes for the different factors tested were changed to see if this had any major artifactual impact on the conclusions. Abundance data were unavailable for six samples from Pierre Noire and for all samples from HEBBLE and Puerto Rico.

Analytical Methods

Rarefaction curves (Sanders 1968) were calculated for all samples from the 17 sites using the methods of Hurlbert (1971). It is important to plot the whole curve for each sample to check for anomalous outriders or groups and to check that the analysis was not compromised by grossly crossing curves (Simberloff 1972). Once this criterion was satisfied, composite curves were created for each biotope by averaging the results for each sample-size "knot" on the curve for each biotope. The final summary figures comparing the composite rarefaction curves for each biotope were then prepared, with the extensions of the curves past *ES*(91) for the larger samples omitted to facilitate comparison. These composite curves compare alpha-diversity from each biotope; they do not indicate the number of different species found in a "region."

Several diversity indices were calculated and their values blocked according to different criteria (see Table 1). Diversity indices do not necessarily rank samples in the same order (Lambshead et al. 1983). The major difference occurs between indices that are weighted for species richness and those that are weighted for equitability (evenness, the opposite of dominance). There is a considerable literature on the individual merits of these indices (Heip et al. 1988), but no consensus of opinion emerges. We have used five commonly employed indices. Margalef's species-richness-weighted diversity index *SR* (Margalef 1958; using logbase *e*) was calculated using $SR = (S - 1)\,1nN$, where S is the number of species and N is the number of individuals in the sample. The species-richness-weighted Shannon information function H' (Pielou 1975; using logbase 2) was calculated using $H' =$ sum of $-P^i \mathrm{Log}_2 P^i$ for each species, where P is the proportion of the sample occupied by that species. Species-richness-weighted rarefaction calculations (Sanders 1968; Hurlbert 1971; Simberloff 1972) were used to derive two indices *ES*(51) and *ES*(91), the expected number of species in a "standardized" sample of 51 and 91 individuals, respectively. Two knots, 51 and 91, were used because many of the samples were 100 or more (hence 91), but 13 deep-sea samples were smaller, requiring a cut of 51 to allow their inclusion in the analysis. There is some advantage to be gained in using two numbers because the fact that rarefaction cores can cross means that different knot levels can rank samples differently. Equitability was calculated using the equitability weighted index J' (Pielou 1975; using logbase 2), where $J' = \mathrm{H}'/\mathrm{Log}_2 S$. Equitability was also calculated by the Ewens-Caswell neutral-model statistic V, using logbase *e*, where $V = [H' - E(H')]/[\mathrm{Sd}.\ E(H')]$. $E(H')$ is the expected value of H' for a theoretically neutral sample unaffected by biological interactions or disturbance (Ewens 1972; Caswell 1976; Lambshead & Platt 1988; Goldman & Lambshead 1989). The Ewens-Caswell statistics (V) and *ES*(X) have the advantage of being robust to sample size differences, whereas some of the other indices, notably H', are notoriously influenced by sample size.

Statistical analyses of the indices were carried out using Statgraphics V+ (STSC 1991). ANOVA analysis was used to determine whether biotopes were significantly different according to environmental or artifactual factors, and multifactor ANOVA (MANOVA) was applied to test which factors might be important (data blocked into classes, see Table 1). The analysis for unbalanced experimental designs was employed with no high-level interactions (>1) using least-squares difference (LSD). Multiple-range tests (LSD) indicated which variables were significantly different (at $p < 0.05$).

Results

The composite rarefaction curves for alpha diversity for each biotope are summarized in Fig. 1. The composite curves failed to cross, indicating that it is sensible to compare them. The lowest diversity was shown by the temperate estuarine and hadal biotopes. The tropical and temperate sublittoral biotopes were more diverse. The highest diversities were in the deep-sea abyssal and bathyal biotopes.

For all indices, ANOVA demonstrated highly significant differences among biotopes ($p < 0.000$; Fig. 2). Changing the number of classes and cut levels in the way the data were blocked caused no major changes in the results, so only the analysis for the first classes and cut levels chosen are reported here. The significance or nonsignificance of the differences between the indices for the biotopes according to multiple-range tests are shown in Table 2.

The weighted diversity indices for species richness (Fig. 2) showed a similar pattern to that of Fig. 1, a high Bathyal diversity declining with both increasing and decreasing depth. In shallow water the lowest diversity was recorded from the temperate estuarine biotope. The tropical biotope displayed a similar or lower diversity than the temperate sublittoral, depending on the index employed. The deep-sea samples, showed a declining diversity with depth from the bathyal biotope to the hadal biotope. But not all of these results were significant at the $p = 0.05$ level (Table 2). The temperate estuarine biotope had a significantly lower diversity than the temperate sublittoral biotope for all the weighted diversity indices for species richness. But it was significantly lower than the tropical sublittoral biotope for *SR, ES*(51)

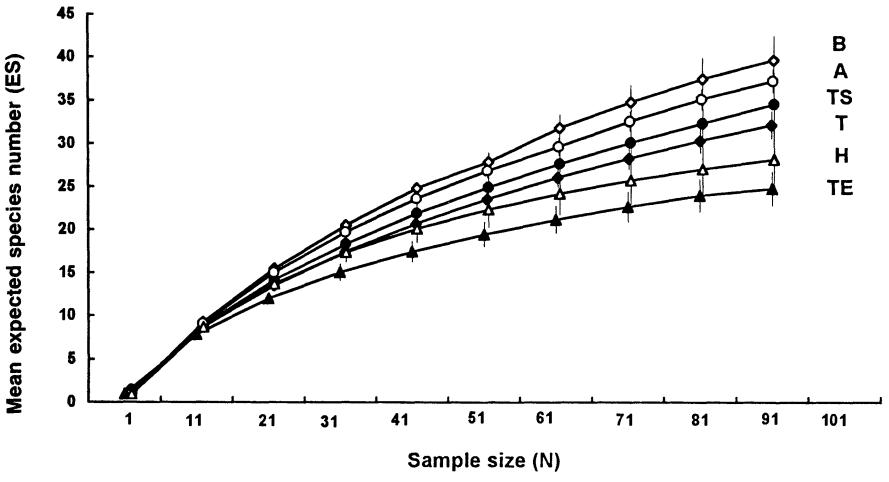

Figure 1. Composite rarefaction curves for the six biotopes. The composite curve was created by calculating the mean and standard error for all the individual abundance "knot" levels (for example, ES(1), ES(11), ES(21)....) for each sample from each biotope (B = bathyl, A = abyssal, TS = temperate-sublittoral, T = tropical-sublittoral, H = hadal, TE = temperate estuarine).

and *ES*(91) but not *H′*. The two sublittoral biotopes were not significantly different for any of the species-richness weighted indices, except *H′*. The most diverse biotope, the bathyal, was significantly more diverse than the temperate estuarine and tropical sublittoral biotopes for all species-richness weighted indices. The bathyal biotope was significantly more diverse than the temperate sublittoral for *ES*(51) and *ES*(91) but not *SR* or *H′*. The bathyal biotope was not significantly more diverse than the abyssal biotope but was significantly more diverse than the hadal biotope for all weighted diversity indices for species richness. The abyssal biotope was significantly more diverse than the hadal for *SR*, *ES*(51), and *ES*(91) but not *H′*.

The equitability indices did not show a consistent pattern. The equitability index (*J′*) was similar from biotope to biotope except for the low value recorded for the temperate estuarine, which was significantly lower than all biotopes apart from temperate sublittoral (Fig. 2). The *V* statistic had a pattern inverse to that of the weighted diversity indices for species richness, with the temperate sublittoral and bathyal biotopes having the lowest equibility. Little of this pattern showed statistical significance, however, except that the abyssal and hadal biotopes were significantly more equitable than the sublittoral biotopes. The standard error of the mean for *V* was higher than the other indices tested (Fig. 2).

As well as biotope, ecological factors showed a pronounced influence on the diversity indices whose mean values were significantly different according to depth, sediment type, core penetration, and abundance. For example, the diversity in sandy sediments was tested against that of muddy sediments for all indices. The ANOVA results (Table 3) showed that sand samples were significantly less diverse and equitable than mud samples for all indices except *J′*. It seemed possible that this result was biased by the fact that all the deep-sea samples were classed as mud. The analysis was therefore repeated with these samples omitted. This shifted the balance slightly in favor of the sand samples in that *ES*(*X*) and *V* were now not significantly different when sand and mud samples were compared and sand samples showed a significantly higher evenness as measured by *J′*.

MANOVA suggested that more than one factor contributed to the results (Table 4) but showed granulometry to be unimportant. *SR* and *H′* were highly significantly

Table 2. Multiple-range analysis produced by ANOVA for each of the six diversity and equitability indices for each biotope.[a]

Biotype[b]	*SR*	*H′*	*J′*	*ES(51)*	*ES(91)*	*V*
TE	*	*	*	*	*	**
T	**	*	**	*	*	*
TS	**	**	**	*	**	*
B	*	*	**	*	*	**
A	**	**	*	*	**	*
H	**	**	***	**	**	*

[a] *Asterisks in the same columns indicate homogenous groups—that the biotopes are not significantly different at the level of p = 0.05.*
[b] *TE = temperate-estuarine, T = tropical-sublittoral, TS = temperate-sublittoral, B = bathyl, A = abyssal, H = hadal.*

Table 3. ANOVA analysis comparing diversity of sand samples against mud for the six indices for all the samples and for shallow-water samples only.

Index	*Comparison of sand versus mud**	*Probability*
SR	all <	0.000
	shallow <	0.001
H′	all <	0.000
	shallow <	0.014
J′	all ——	0.609
	shallow <	0.001
ES(51)	all <	0.000
	shallow ——	0.359
ES(91)	all <	0.002
	shallow ——	0.289
V	all <	0.035
	shallow ——	0.905

** < = significantly less than; > = significantly greater than; —— = no significant difference at the level of p = 0.05.*

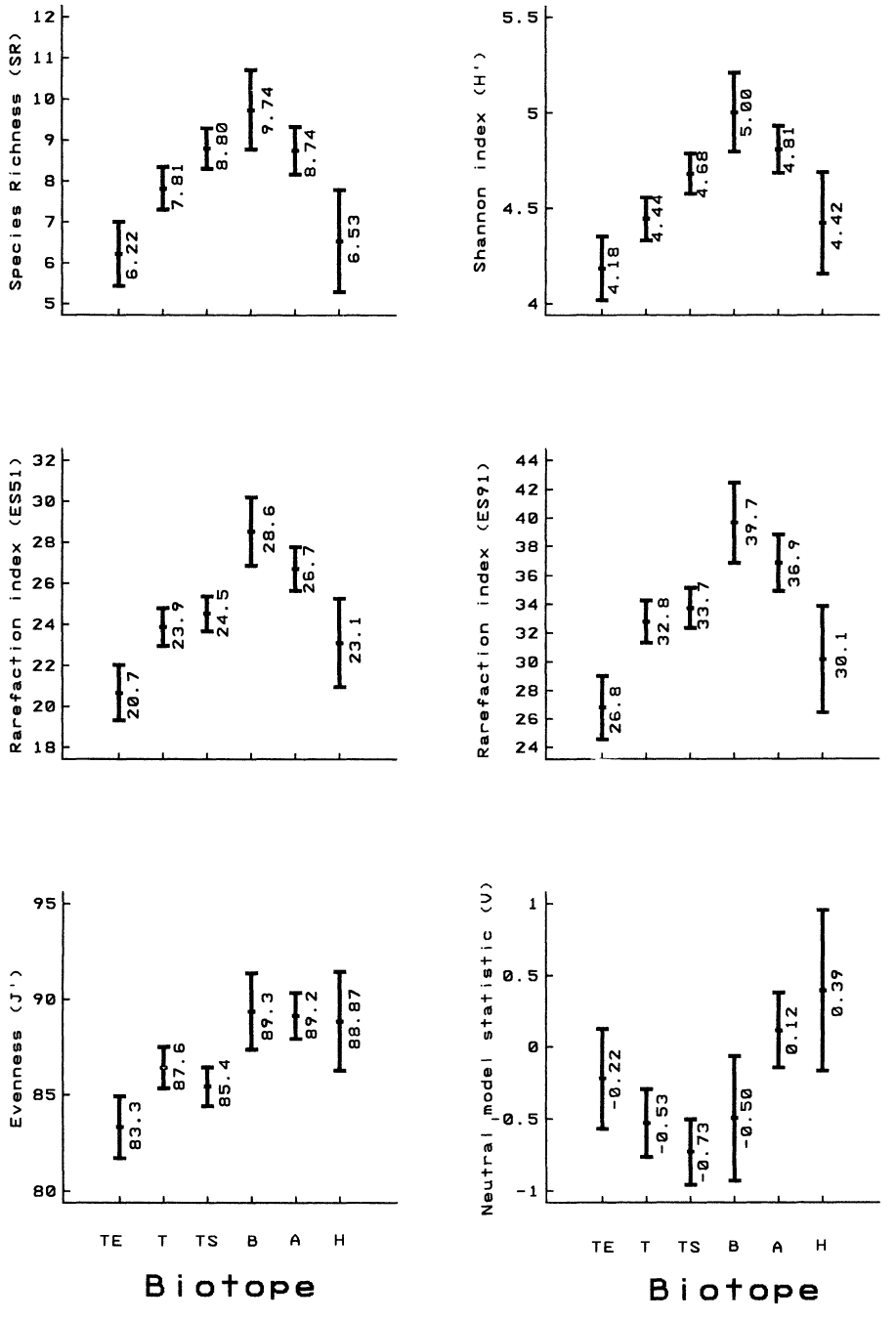

Figure 2. The mean and standard error of the mean for the six diversity indices for each biotope. See Fig. 1 legend for biotope definitions.

influenced by depth (Fig. 2), abundance (negative), and sample size (positive). Results for *ES*(*X*) were similar, except, as expected, *ES*(*X*) was not significantly affected by sample size, but *ES*(91) was significantly affected by core penetration. The equitability index (J') was significantly influenced by depth (Fig. 2), abundance (negative, and sample size (negative). The *V* statistic showed no significant influence by any of the factors tested.

Discussion

It is clear from the ANOVA and multiple-range tests that the biotopes, selected here on the basis of depth and latitude, were significantly different from each other for both species-richness weighted diversity and equitability indices. But differences in diversity may be governed by artifacts associated with sampling (such as sample size and core penetration) or by some major ecological factor governing diversity, that is nonrandomly distributed among the biotopes.

The major sampling artifacts tested here were sample size and core penetration. The robustness of *ES*(*X*) and *V* to sample-size effects is an important factor in their favor. For the species-richness weighted indices, H' and *SR* gave a similar pattern to that of *ES*(*X*) (Fig. 2), but there were some noteworthy differences (Table 2). H'

Table 4. Level of significance of multifactor analysis of variance (MANOVA) for the six diversity indices against ecological factors.

Factor	*SR*	*H′*	*J′*	*ES(51)*	*ES(91)*	*V*
Depth	0.000*	0.000*	0.000*	0.000*	0.000*	0.101
Abundance	0.000*	0.000*	0.000*	0.000*	0.000*	0.459
Sediment type	0.696	0.846	0.812	0.756	0.660	0.786
Sample size	0.000*	0.045*	0.007*	0.877	0.622	0.073
Core penetration	0.576	0.167	0.180	0.052	0.038*	0.806

**Significance at 0.05 level.*

did not distinguish between abyssal and hadal biotopes. Also, H' suggested that the tropical sublittoral biotope had a significantly lower biodiversity than the temperate sublittoral biotope. (The same pattern was displayed by SR but was not significant). It is suspicious that the tropical samples tended to have a smaller sample size than the temperate ones, and we consider this result to be an artifact. Therefore, we conclude that *ES* is superior to H' and *SR* and that *V* is better than J', wherever sample-size variations could prejudice results.

Previous work has indicated vertical zonation of nematode populations, both quantitatively and qualitatively, at different sediment depths (Boucher 1972; Jensen 1987). Both decreasing and increasing diversity has been recorded (Ott 1972; Boucher 1980; Boucher & Gourbault 1990) according to sediment depth. But the degree of core penetration seems not to have had a detectable influence on the indices tested here, except possibly for *ES*(91). This may explain why *ES*(91) gave a slightly lower degree of resolution between the biotopes than *ES*(51).

The number of nematodes per unit area showed a highly significant association with diversity for all indices except *V*. Because abundance is a crude estimate of production, this suggests that production has an important influence on nematode diversity. At the scales investigated here, production is closely associated with depth. The flux of organic material into deep-sea sediments depends on water depth and distance from shore, which—because of the shape of the ocean basins—tend to covary, so water depth alone is closely correlated with declining nematode abundances (Lambshead et al. 1994). Conversely, some of the highest nematode abundances ever recorded have been from temperate estuaries, such as 13.3 million/m^2 (Warwick et al. 1979). Clearly, abundance and depth are strongly correlated, so we consider them together.

Sediment type is commonly considered to be correlated with nematode diversity: sandy sediments have higher diversities than muddy sediments (Ferris & Ferris, 1979; Heip et al. 1982, 1985). An inverse correlation between species diversity and silt-clay content has often been demonstrated (Heip & Decraemer 1974; Tietjen 1977) because of the significantly richer fauna in coarser sediment. Similarly, a correlation between faunal diversity and sediment diversity has been shown for deep-sea macrofauna (Etter & Grassle 1992). Tietjen ascribed lower nematode *SR* value of silty sediments to a reduction in the number of trophic types. Contrary to all expectations from the literature, our results indicate that nematode assemblages in sand samples are not more diverse than in mud samples. Indeed, our results suggest that the reverse may be true. Apparent correlations between granulometry and diversity may well be caused by the intrusion of other factors. For example, the association between muds and low nematode diversity may have sometimes arisen because the muddy sediments investigated were from estuaries and polluted sites and hence exhibited low diversity because of physically demanding local ecological conditions. Sublittoral muddy sediments, such as represented by the Banyuls data, can produce samples exhibiting high nematode diversity. This conclusion is supported by research on copepods, the second most abundant and speciose metazoan meiofauna group. Coull and Fleeger (1977) investigated a mud sublittoral site and a sand sublittoral site within 1 km of each other and found no significant differences in copepod diversity. A number of authors have since confirmed this finding (Hicks & Coull 1983).

Biotope Diversity

Species-Richness Weighted Indices

The relationship between depth and diversity was nonlinear and almost certainly connected with the association between depth and production. The weighted diversity indices for species richness show an increase in diversity with depth down to bathyal-abyssal depths, after which there is a decrease in diversity in the hadal biotope. This nonlinear depth relationship is interesting because a number of authors have suggested a parabolic curve for the relationship between species richness and depth for meiofauna (Dinet & Vivier 1979) and macrofauna (Rex 1976, 1983; Huston 1979; Maciolek et al. 1987*a*, 1987*b*; Paterson 1993; Paterson et al. 1995). The diversity of copepods appears to generally follow that of nematodes in that there is an increase from shallow waters to the deep sea (Coull 1972; Thistle 1978).

Dinet and Vivier (1979) reported a peak in meiofauna diversity at 4000 m. The peak of the macrofauna diversity curve with depth is not consistent from study to study but occurs roughly in the bathyal region. The processes causing these depth-diversity relationships are not well understood, and it is possible that different factors are important for different taxa and locations. Essentially the curves seem to involve a nonequilibrium interaction (Connell 1978) between production and disturbance as described by Huston (1979). Rex (1976) suggested that intraspecific predation was the disturbance agent in his northwest Atlantic data, while Paterson et al. (1995) concluded that water current was the disturbance agent in the northwest Atlantic. It is not clear what the distur-

bance agent might be for nematodes, but it is unlikely that intraspecific predators were responsible because predatory nematodes were rare in bathyal samples; equally, the bathyal nematode samples show no evidence of current disturbance effects (Lambshead et al. 1994).

The low diversities found in the temperate estuarine and hadal biotopes are probably the consequence of physical disturbance. Both these biotopes are subject to high degrees of physical disturbance. Deep-sea trenches have extremely low secondary productivity as well as high disturbance in the form of sediment collapse from the canyon walls.

One unexpected latitudinal result is that the tropical sublittoral mean is not higher than the temperate sublittoral mean (see also Boucher 1990). However, there are other studies to support this finding. Soil nematodes have been found to be more diverse at higher than at lower latitudes (Procter 1990). In their extensive review, Hicks and Coull (1983) conclude that, in the absence of strong local environmental factors (such as salinity) influencing copepod diversity, "comparable diversities can be anticipated in shallow sedimentary biotopes worldwide." Kendall and Aschan (1993) failed to discover a latitudinal diversity difference for shallow-water macrofauna. In contrast, Rex et al. (1993) found latitudinal diversity gradients in the North Atlantic for deep-sea benthic macrofauna, with diversity declining polewards.

Equitability

The equitability indices were less capable of discriminating between biotopes and had more variation between samples (higher standard errors) than the species-richness weighted indices. This was especially true of V which, on grounds of sample-size independence, should be the more accurate of the two measures. It appears that in this study the species-richness component of diversity contained more biotope information than the equitability component of the species-richness weighted indices.

The V statistic has proved to be effective as an indicator of natural and anthropogenic disturbance in a variety of situations (Platt & Lambshead 1985; Paterson et al. 1995), demonstrating that it is sensitive to local environmental processes; this may be generally true of equitability weighted indices (Shaw et al. 1983). Thus, equitability may be less suitable than species richness for comparing alpha diversity between large scales such as biotopes or regions.

Conclusions

The marine environment covers two-thirds of the earth, but these 17 standardized data sets, despite representing an enormous outlay of scientific time and expertise by various investigators, are taken from only about 0.5 m^2 of sediment surface. This limitation must be borne in mind when considering our conclusions. Nematodes are able to maintain populations in extreme physical conditions where other taxa, especially macrofaunal taxa, are eliminated (Heip 1980; Pearson 1980), which is one of the reasons they are such a useful tool for environmental research. But given their robustness to detrimental conditions, it is unclear how far analyses of nematode diversity are applicable to other fauna, although there is a degree of concordance between our results and studies of copepods and macrofauna taxa.

Alpha or sample diversity only was analyzed in this study. This is an important statistic, particularly in the area of environmental monitoring, but it does not necessarily provide insight into regional or biotope species pools. It is likely, however, that high alpha diversity will correlate with high beta diversity, all other things being equal. A regional-biotope species-pool estimation for marine nematodes is not possible without a major taxonomic investigation into species turnover in different communities.

We conclude that marine nematode diversity is significantly different among the large-scale biotopes chosen for this study. Local ecological factors can have a tremendous influence, however, especially on equitability, and this should be taken into account in biodiversity investigations that focus on alpha diversity. Species-richness weighted indices, rather than equitability indices, are therefore to be recommended for large-scale comparisons. Sample size has a significant artifactual impact, so indices such as $ES(X)$ that are robust to sample size are recommended. There is a nonlinear relationship between depth and diversity, with bathyal and abyssal samples having the highest diversity. Tropical sublittoral nematode samples show no evidence of higher diversity than equivalent temperate samples. The most physically challenging biotopes, temperate estuarine and hadal, display the lowest diversities.

This study lends more evidence to the recent view that the bathyal and abyssal benthic biotopes are one of the high-diversity environments (Grassle 1989; Lambshead 1993). Because these environments are relatively simple, in that they have a limited number of critical processes influencing biodiversity, they offer an opportunity to study how processes maintain high biodiversity over ecological time scales. Nematode communities give appropriate data for statistical discrimination of the patterns associated with such diversity-maintaining processes. An understanding of these processes is vital for the conservation of healthy, diverse habitats.

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