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NEMATODA
DEEP-SEA BENTHOS
FUNCTIONAL GROUPS

ABSTRACT – Although it has been proposed that tail shapes could be used as the basis for ecologically useful functional groups of nematodes, the proposition has not been tested. We used data from three sites in the deep North Atlantic for such a test. In a pretest, we found that nematode functional groups based on buccal morphology differed significantly in their proportional representation among the sites, indicating that for nematodes the sites differed ecologically. Results of similar tests involving tail-shape groups were significant, indicating that there is ecological information in the tail-shape groups, and a further test revealed that the information in the shape of the tail was not a simple reflection of information in the buccal-morphology groups. Distribution of functional groups formed by combining tail shape and buccal morphology also differed significantly among sites. We conclude that both the tail-shape and buccal-morphology-by-tail-shape approaches hold promise for the ecological analysis of deep-sea nematode assemblages.

NEMATODA
BENTHOS PROFOND
GROUPES FONCTIONNELS

RÉSUMÉ – Bien que la forme de la queue des Nématodes ait été proposée pour constituer des groupes fonctionnels sur le plan écologique, cette hypothèse n'a pas été testée. Nous avons utilisé des données provenant de trois sites de prélèvements de l'Atlantique nord profond pour de tels tests. Dans un test préliminaire, nous avons trouvé que les groupes fonctionnels de Nématodes basés sur la morphologie buccale présentaient des différences significatives dans leurs proportions relatives entre les sites, ce qui montre que les sites sont différents sur le plan écologique pour les Nématodes. Les résultats d'analyses similaires impliquant les groupes constitués à partir de la queue sont significatifs, indiquant qu'il existe une information d'ordre écologique à partir de ces groupes et une analyse ultérieure montre que l'information provenant de la forme caudale ne correspond pas à une simple redondance de l'information obtenue à partir des groupes basés sur la morphologie buccale. La distribution des groupes fonctionnels obtenus en combinant la forme caudale et la morphologie buccale diffère également de façon significative entre sites. En conclusion, les deux approches, forme caudale et morphologie buccale – forme caudale seront intéressantes à exploiter lors des analyses écologiques des communautés de Nématodes profonds.

INTRODUCTION

That nematodes are an important component of the deep-sea soft-bottom fauna can be argued many ways. They are by far the most abundant metazoans, and they constitute a nonnegligible portion of the biomass (Gage & Tyler, 1991). They are thought to feed primarily on microbes (Jensen, 1988), although predators are known (Jensen, 1992). They are probably food for larger organisms and so play a role in deep-sea food chains, but only inferential evidence is available (Lambshead *et al.*, in press). In shallow water, they alter the sea bed by adding mucus (Riemann

and Schrage, 1978), by creating burrows (Cullen, 1973), and by tube-building (Nehring *et al.*, 1990; Nehring, 1993); deep-sea nematodes may have similar effects. Despite the importance of nematodes, our understanding of their ecology in the deep sea lags that of other groups; we are still in the pattern-recognition stage. One reason for this situation is that deep-sea nematodes are extremely diverse (Lambshead, 1993), and most species are rare, making the acquisition of ecological information difficult.

One approach to this problem has been to combine species into functional groups. Functional groups consist of species that share morphological

traits thought (or known) to imply similarity in an important ecological function. For nematodes, Wieser (1953) proposed that buccal morphology could be used to group by feeding type. This scheme has been widely used in ecological work (see references in Jensen, 1987, and Tietjen, 1989). Thistle and Sherman (1985) noted that nematode tails could be important in locomotion and reproduction and proposed a second functional grouping of nematodes based on tail shape. To date, the ecological utility of nematode tail-shape groups has not been tested. In this paper, we first use the buccal-morphology approach to show that our sites differ ecologically from the perspective of nematodes. We then test the ability of tail-shape groups to detect differences among the sites that are not simply those reflected by the buccal-morphology groups. We also tested the proposition that tail-shape grouping and buccal-morphology grouping could be combined to give an ecologically useful, two-way classification for nematodes analogous to that for polychaetes (Jumars and Fauchald, 1977).

METHODS

Site descriptions

Two of the sites are in the northeast Atlantic and were studied as part of the MAST-funded, multidisciplinary investigation into the effects of seasonal flux of phytodetritus to the sea floor. The sites were chosen to differ as little as possible except for the depth of winter mixing in the overlying water and are described in detail by Rice and Lambshead (1993, see their Fig. 15.2), Lambshead and Hodda (1994), Rice et al. (1994), and Lambshead et al. (in press). The Porcupine Abyssal Plain site (PAP) is located to the southwest of Ireland at 4850 m depth (48° 50′ N, 16° 30′ W). It receives a major seasonal input of aggregated phytodetritus. The second station (MAP) is located on the Madeiran Rise at 4950 m depth (31° 05′ N, 21° 10′ W). Time-series bottom photographs show that MAP lacks the phytodetritus flux experienced at PAP and has lower biological activity. Standing stocks at MAP are also lower than those at PAP (Thurston et al., 1994).

The site we will refer to as "HEBBLE" is located in the northwest Atlantic at the base of the Scotian Rise at 4626 m depth (core 1, 40° 24.0′ N, 63° 07.4′ W; core 2, 40° 24.3′ N, 63° 09.6′ W). It was the location of preliminary studies for the High Energy Benthic Boundary Layer Experiment (Hollister and Nowell, 1991); the actual HEBBLE site was 69 km away at 4820 m and is described by Thistle et al. (1991). The two locations have similar environments, so we have used information from both in this description. The productivity of the overlying water is relatively high (Berger, 1989, his Fig. 11), and some evidence suggests that the food supply to the benthos is abundant (Hollister and Nowell, 1991). The near-bottom hydrodynamic regime is dramatically different from that of quiescent

deep-sea sites. In particular, the site is exposed to benthic storms during which maximum velocities at 10 m above bottom reach 15-40 cm s^{-1} (Weatherly and Kelly, 1982; Hollister and Nowell, 1991). Eight to 10 storms occur annually. During storms, millimeters of sediment can be eroded; during interstorm periods, similar amounts are deposited.

Sampling

At both PAP and MAP, one core (5.7 cm internal diameter) was chosen from each of six multiple-corer lowerings (Barnett et al., 1984). The top 1-cm layer of sediment was immediately fixed in buffered, seawater formalin (9 :1, v :v). In the laboratory, the nematodes were extracted by a modification of the Ludox-TM-decantation method (de Jonge and Bouwman, 1977) (45-μm sieve), placed in functional groups, and enumerated (Tables I and II).

Table I. – Porcupine Seabight nematodes by buccal morphology and tail shape. See text for the meaning of abbreviations. Samples are from station 11908 (Rice et al., 1994).

Tail Shape	Sample 1	2	3	4	5	6	Buccal Morphology
1	18	19	18	23	6	6	
2	61	41	51	90	17	10	1A
3	9	21	49	13	3	6	
4	29	22	52	29	2	8	
1	1	1	1	0	2	0	1
2	27	55	25	42	6	7	1B
3	1	0	1	1	0	0	
4	5	5	2	8	1	0	
1	0	0	0	0	0	0	
2	2	0	23	4	1	2	2A
3	52	29	47	24	15		
4	34	27	64	51	14	31	
1	0	0	0	0	0	0	
2	0	0	0	0	5	0	2B
3	1	0	0	0	0	0	
4	6	6	5	6	4	2	3

Table II. – Madeira Abyssal Plane nematodes by buccal morphology and tail shape. See text for meaning of abbreviations. Samples are from station 12174 (Rice *et al.*, 1994).

Tail Shape	Sample 1	2	3	4	5	6	Buccal Morphology
1	0	1	0	0	1	0	
2	36	53	21	24	13	13	1A
3	4	13	5	5	1	3	
4	6	23	3	7	5	2	
1	0	0	0	1	0	0	
2	24	41	16	9	8	7	1B
3	1	1	0	0	0	0	
4	3	3	3	0	4	1	
1	0	0	0	0	0	0	
2	11	7	7	4	4	8	2A
3	6	5	5	3	5	1	
4	9	10	10	7	4	11	
1	0	0	0	0	0	0	
2	0	0	2	1	0	0	2B
3	0	0	0	0	0	0	
4	26	30	8	8	18	7	

The HEBBLE samples were taken with a 0.25-m^2 box corer (Hessler and Jumars, 1974); two box cores were taken 3 km apart. We studied the central nine 10-cm-by-10-cm subcores (Thistle *et al.*, 1985, their Fig. 3) from each box core. Because each subcore contained a subsubcore for use by another investigator, 77 cm^2 per subcore was sampled for nematodes. At sea, the water overlying each subcore was drawn off and passed through a 45-μm sieve. The top 1 cm of each subcore and the sieve residue were preserved in sodium-borate-buffered seawater formalin (4 :1, v :v). In the laboratory, each sample was washed on a 62-μm sieve (the fraction passing a 62-μm sieve and caught on a 44-μm sieve from two subcores selected at random contained < 1 % of the nematodes; this fraction was not considered further.) Thistle and Sherman (1985) described how a random 25 % subsample of the nematodes in each sample was obtained (Tables III and IV).

Because the HEBBLE samples were collected with a box corer and the MAP and PAP samples with a multiple corer, the possibility that faunal differences could arise from differences in sampler performance had to be confronted. Bett *et al.* (1994) point out that, in general, box corers collect nematodes less efficiently than multiple corers, at least in part because the pressure wave that precedes a box corer displaces material of low specific gravity (*e.g.* nematodes) from the surface of the sediment before the sample is taken (Jumars, 1975). However, the box corer employed had been modified to reduce bow-wave effects (see Thistle and Sherman, 1985, for details). Also, the HEBBLE site frequently experiences strong benthic storms that reduce the amount of easily displaced material on the sediment surface (*in situ* photographs, personal observation, D.T.). Thistle and Sherman (1985) tested for evidence of the displacement of nematodes from the HEBBLE samples and found no evidence for it, implying that the samples were taken during one of the many periods when the HEBBLE-site sediments cannot be eroded, even by benthic storms (Gross and Williams, 1991). Bow-wave-induced bias appears to have been minimal.

Morphological groups utilized

Wieser (1953) proposed that buccal morphology could be used to group marine nematodes into four groups that fed in similar ways : 1A = small/absent buccal cavity without teeth, 1B = medium/large buccal cavity without teeth, 2A = small/medium cavity with teeth, and 2B = large buccal cavity with large teeth/mandibles. This classification has proved to be of great value and has often been employed in shallow-water (*e.g.* see references in Heip *et al.*, 1985, and Jensen, 1987) and deep-sea studies (Rutgers van der Loeff and Lavaleye, 1986). In the deep sea, Wieser's groups have been used primarily to explore the responses of nematodes to differences in sediment texture and composition (Tietjen, 1989, and included references).

Wieser (1953) suggested four functions for the feeding groups – 1A = selective deposit feeders, 1B = nonselective deposit feeders, 2A = epistrate feeders, and 2B = omnivore-predators – but additional information on the feeding behavior of shallow-water (*e.g.* Tietjen and Lee, 1977; Jensen, 1979, 1982, 1986, 1987; Romeyn and Bouwman, 1983; Romeyn *et al.*, 1983, Nehring, 1992a, b) and deep-sea nematodes (Jensen, 1992) has become available. These observations, albeit on a limited number of species, have not entirely supported the originally suggested feeding behavior for Wieser's groups. For example, Romeyn and Bouwman (1983) reported that some species with 1A buccal-cavity types (*e.g. Monhystera microphthalma*) were actually nonselective feeders. Information on feeding in the 2B group has indicated that it includes both true predators, which ingest prey, and scavengers. The latter are the families Oncholaimidae and Enchelidiidae, which are only partially predatory as adults (without ingesting prey) and not at all predatory as juveniles (Jensen, 1987, and references therein; Riemann and Schrage,1978).

These observations have lead to suggested modifications to Wieser's morphological groups. Romeyn and Bouwman (1983) and Bouwman *et al.* (1984) included sensory organs as additional characters for delineating trophic groups, but this approach has not been widely supported and is rejected by Jensen (1986, 1987). Jensen (1986, 1987) suggested splitting the 2B group into true predators and scavengers. He also recommended

Sample

Tail Shape	7	8	9	12	13	14	17	18	19	Buccal Morphology
1	0	0	0	0	0	3	1	0	0	
2	6	3	11	6	15	15	28	21	14	1A
3	5	2	3	3	5	6	8	9	6	
4	8	4	12	23	17	16	19	14	17	
1	0	0	0	0	0	0	0	0	0	
2	9	1	2	3	3	0	5	1	6	1B
3	0	1	4	0	0	0	4	7	2	
4	27	5	27	44	18	26	35	50	23	
1	0	0	0	0	0	0	0	0	0	
2	0	0	15	13	24	23	42	19	12	2A
3	8	5	9	10	6	16	15	22	28	
4	4	3	1	16	5	9	6	5	1	
1	0	0	0	0	0	0	0	0	0	
2	2	5	4	8	8	20	7	7	5	2B
3	0	0	0	0	0	0	0	0	0	
4	0	2	2	7	2	4	9	5	4	

Table III. – Nematodes from the first HEBBLE box core. The sample numbers refer to the position of the subcores in the corer box (see Thistle *et al.*, 1985, their Fig. 3). See text for meaning of abbreviations.

combining groups 1A and 1B on the grounds that the morphological distinction between the two groups was arbitrary and not indicative of a fundamental trophic distinction.

In this paper, we elected to use the original buccal-morphology groups of Wieser. This approach allowed us to test whether it is useful to preserve the distinction between the 1A and 1B groups. Also, although the case for dividing the 2B group into scavengers and true predators (Jensen, 1986, 1987) is strong, at our sites, as in other deep-sea studies (Jensen, 1988), scavengers were extremely rare; we therefore retained the 2B classification as a single group for statistical purposes.

Thistle and Sherman (1985) proposed that nematodes could also be usefully grouped by tail shape, given that tail shape plays an important role in nematode biology, *e.g.* for locomotion (Adams and Tyler, 1980) and reproduction (J.L. personal observation). However, the functional significance of only one of their groups was known. That is, Riemann (1974) reported that long-tailed nematodes were hemisessile, spending substantial periods anchored by the tip of the tail to the substrate by an adhesive secreted by the caudal glands. Note that long-tailed nematodes have been considered to be an ecological group by other workers (*e.g.* Fegley, 1987).

Thistle and Sherman (1985) created 11 morphological tail-shape groups based on the HEBBLE specimens.

In attempting to apply this scheme to the PAP and MAP specimens, we realized that many of the categories intergraded (see also Bussau, 1993) and that the eleven tail-shape groups could be reduced to four (Fig. 1). These are the "rounded" tail type, with a blunt end (tail-shape 1; Thistle and Sherman's category A); the "cla-vate-conicocylindrical" tail type, initially conical with an extension to the tip (tail shape 2; Thistle and Sherman's categories B and E); the "conical" tail type, with a pointed tip and tail length less than five body widths (tail shape 3; Thistle and Sherman's categories D, F, H, J, and K); and the "long" tail type, with a tail longer than five body widths (tail shape 4; Thistle and Sherman's categories C, G, and I).

Statistical analysis

For a given method of grouping (by buccal morphology, tail shape, or both simultaneously), we tested the null hypothesis that the nematodes at the three sites were distributed in the same proportion among the categories of the group with a row-by-column test of independence using the G-test (Sokal and Rohlf, 1969). We explored the data by calculating bootstrap (Efron and Gong, 1983) 95 % confidence intervals (N = 1 000) for the median of the percent abundance of each category

Tail Shape	Sample 7	8	9	12	13	14	17	18	19	Buccal Morphology
1	1	0	0	0	0	0	0	0	0	
2	9	9	14	13	13	14	9	12	23	1A
3	5	8	8	7	5	9	8	6	28	
4	4	10	17	12	13	14	15	17	17	
1	0	0	0	0	0	0	0	0	0	
2	7	6	2	5	4	8	3	4	1	1B
3	12	1	1	7	3	2	5	6	15	
4	11	29	36	18	25	16	16	18	39	
1	0	0	0	0	0	0	0	0	0	
2	15	37	17	38	35	21	27	32	37	2A
3	6	12	25	17	25	16	14	13	18	
4	5	6	7	1	4	0	2	0	11	
1	0	0	0	0	0	0	0	0	0	
2	9	16	8	12	27	12	13	18	18	2B
3	2	0	0	0	0	0	0	1	0	
4	7	3	4	4	5	8	4	4	7	

Table IV. – Nematodes from the second HEBBLE box core. The sample numbers refer to the position of the subcores in the corer box (see Thistle et al., 1985, their Fig. 3). See text for meaning of abbreviations.
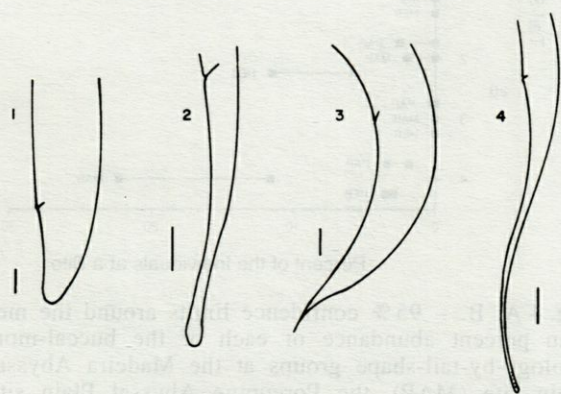

Fig. 1. – Representative tails from each of the tail-shape groups (modified from Thistle and Sherman, 1985) : 1 = rounded, 2 = clavate-conicocylindrical, 3 = conical, 4 = long. Scale lines : 1, 2, and 4 = 20 μm; 3 = 50 μm.

for each station using Resampling Stats (Bruce, 1991). If the 95 % confidence intervals for two medians did not overlap, the medians were considered to be significantly different. In this exploratory analysis, the HEBBLE subcores were treated as independent samples. Also, we did not adjust the alpha level to correct for the increased probability of rejecting a true null hypothesis when multiple tests were performed.

RESULTS

Our test of the utility of the tail-shape approach required that our three sites differ ecologically from the perspective of nematodes. We tested this assumption using the buccal-morphology groups. The test of independence detected a significant (p << 0.005) departure from proportional representation. The sites differed in their buccal-morphology-group composition, as expected if the sites differed ecologically from the perspective of nematodes. By examining the 95 % confidence intervals (Fig. 2), we found that the proportion of group 2B was significantly greater at MAP and at HEBBLE than at PAP and that the proportion of group 1A was significantly less at HEBBLE than at either MAP or PAP.

To test the efficacy of the tail-shape grouping, we repeated the analysis that we had done on the buccal-morphology grouping. The tail-shape groups were not distributed proportionally among the sites (p << 0.005), as expected if the tail-shape groups responded to ecological differences among the sites. In the 95 %-confidence-interval analysis (Fig. 3), we found that the proportions of tail-
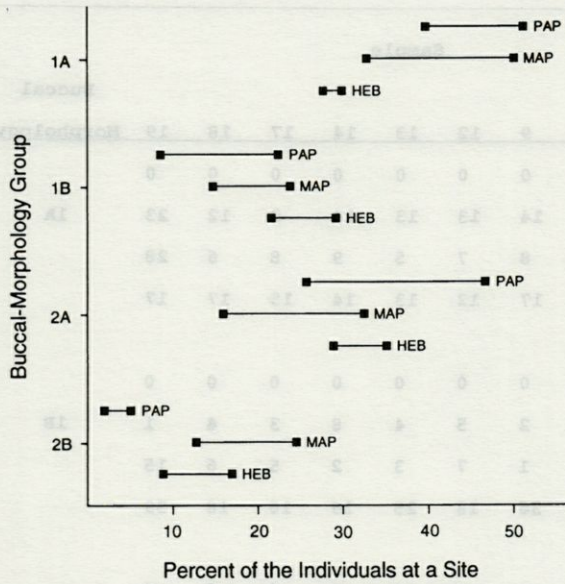
Fig. 2. – 95 % confidence limits around the median percent abundance of each of the buccal-morphology groups at the Madeira Abyssal Plain site (MAP), the Porcupine Abyssal Plain site (PAP), and the HEBBLE site (HEB). See text for explanation of buccal morphology groups. 1A = small or absent buccal cavity without teeth. 1B = medium or large buccal cavity without teeth. 2A = small or medium buccal cavity with teeth. 2B = large buccal cavity with large teeth or mandibles.
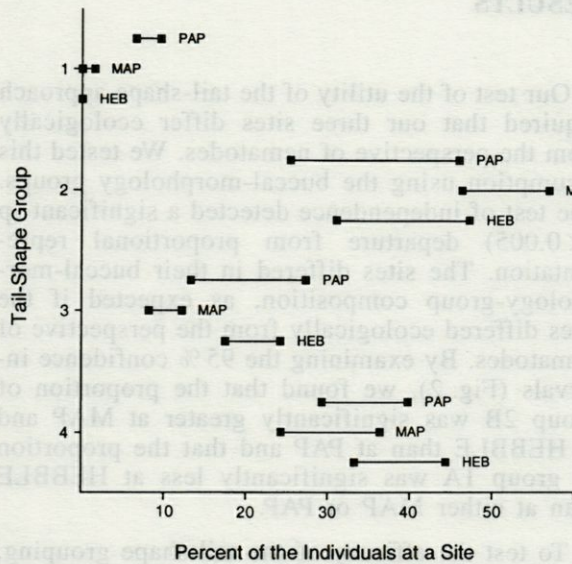

Fig. 3. – 95 % confidence limits around the median percent abundance of each of the tail-shape groups at the Madeira Abyssal Plain site (MAP), the Porcupine Abyssal Plain site (PAP), and the HEBBLE site (HEB). See text for explanation of tail-type groups. 1 = rounded tail, 2 = clavate-conicocylindrical tail, 3 = conical tail, 4 = long tail.
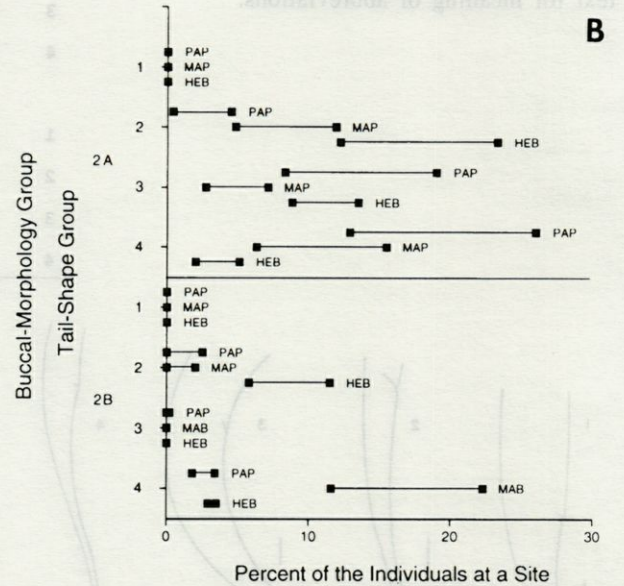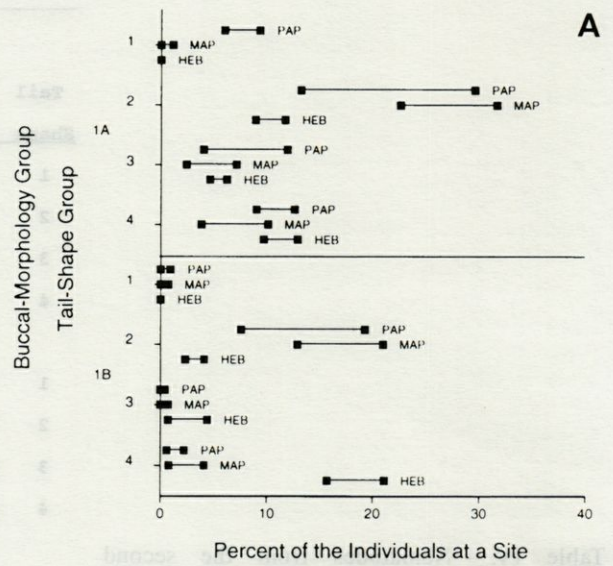

Fig. 4 A, B. – 95 % confidence limits around the median percent abundance of each of the buccal-morphology-by-tail-shape groups at the Madeira Abyssal Plain site (MAP), the Porcupine Abyssal Plain site (PAP), and the HEBBLE site (HEB). See Fig. 2 for explanation of buccal-morphology-group labels. See Fig. 3 for explanation of tail-shape group labels.

shape 1 (rounded) at HEBBLE and at MAP were significantly less than that at PAP, that the proportional representation of tail-shape 2 (clavate-conicocylindrical) was significantly greater at MAP than at PAP, and that the proportional representation of tail-shape 3 (conical) was significantly less at MAP than at PAP or HEBBLE. Five of 12 possible differences (42 %) were significant for tail shape, as were 4 of 12 (33 %) for buccal morphology.

To determine whether the tail-shape groups revealed ecological information not present in the buccal-morphology groups, we proceeded as follows. For a given buccal-morphology group, we ranked the abundance of the individuals by tail-shape group for each of our three sites. If there were no new information in the tail shapes, these rankings should match. We then counted the number of mismatches and repeated the process for each of the buccal-morphology groups. Given four buccal-morphology groups and three sites, there were a total of 12 possible matches. Of these, there were 7 instances of mismatched ranks. The probability of 7 mismatches occurring by chance is much less than 0.005, supporting the inference that there is new information in the tail-shape groups.

To investigate the ecological utility of the two-way grouping, we classified the specimens from each site simultaneously by buccal morphology and tail shape and tested the null hypothesis of proportional representation among the sites. The null hypothesis was rejected ($p \ll 0.005$). The plots of 95% confidence intervals (Fig. 4A, B) revealed that, in 21 of 48 possible pair-wise comparisons among sites (44%), there was a significant difference.

Because of concerns about the comparability of multiple corer (MAP, PAP) and box corer (HEBBLE) samples, we repeated the three tests of independence omitting the HEBBLE data. For all three methods of grouping, the tests remained significant ($p \ll 0.005$), suggesting that the results had not been caused by sampling differences.

DISCUSSION

The sites differed significantly in their buccal-morphology-group composition, suggesting that the sites do differ ecologically from the perspective of marine nematodes, so it was meaningful to use these sites to test the ecological utility of the tail-shape groups. The buccal morphology analysis also showed that the distinction between Wieser's groups 1A and 1B contains ecological information (1A's are significantly rarer at HEBBLE than at the other sites). We recommend retaining this distinction until additional natural-history information allows more biologically meaningful categories to be erected.

Interpretations of the observed differences among sites in relative abundances of buccal morphologies were not the thrust of this paper, but the small representation of 1A's at HEBBLE is suggestive. That is, observations on estuarine 1A nematodes (Romeyn and Bouwman, 1983) suggest that they feed on bacteria by means of continuous

oesophageal pulsations. Feeding can be passively selective, in that the food particles must be small enough to enter the tiny buccal cavity, or more actively selective, in that individual bacteria are chosen. Repeated exposure to benthic storms at HEBBLE may wash from the sediments many of the small particles on which these animals feed.

Our tests revealed that tail-shape groups differed between sites as much as did the established, buccal-morphology groups and that tail-shape groups contained ecological information not incorporated by the buccal-morphology groups, making them potentially useful as ecological tools. A first step toward providing a natural-history underpinning for interpreting tail-shape-group patterns might be to determine how well mode of locomotion is predicted by tail shape (see Adams and Tyler, 1980, and references therein). Until such natural-history information is available, speculation on distribution differences is fruitless except that the absence of a difference in proportional representation of the long-tailed group between HEBBLE and the other sites brings into question Thistle and Sherman's (1985) notion that the hemisessile life style is favored in high-energy areas.

The two-way approach is not more powerful, on a percentage basis, than the single-classification analyses, but it is of interest. First, it shows that tail shape incorporates new information because the two-way classification reveals that particular tail shapes are not restricted to particular buccal morphologies (Fig. 4A, B). Second, with the two-way classification, we discovered some groups to which no species belonged at our sites; there were no 2A's or 2B's with rounded tails. These combinations are known from other environments (e.g. Comesa, Pontonema). Are they absent from the abyss or present in the abyss though absent from our sites? Answers to these questions are relevant to the ecology and evolution of deep-sea nematodes. Finally, the most informative system of functional groups will be the one that corresponds most closely to nematode guilds. Given the diversity of nematodes, the four-subdivision guilds based on buccal morphology and tail shape almost surely underresolve the guild structure. The buccal-morphology-by-tail-shape system may be a step toward this "best" system of functional groups.

REFERENCES

ADAMS P.J.M. and S. TYLER, 1980. Hopping locomotion in a nematode : functional anatomy of the caudal gland apparatus of *Theristus caudasaliens* sp. n. *J. Morphol.*, **164** : 265-285.

BARNETT P.R.O., J. WATSON and D. CONNELLY, 1984. A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanol. Acta*, **7** : 399-408.

BERGER W.H., 1989. Global maps of ocean productivity. *In* Productivity of the ocean : present and past. Edited by W.H. Berger, V.S. Smetacek and G. Wefer, Wiley, New York, 429-455.

BETT B.J., A. VANREUSEL, M. VINCX, T. SOLTWEDEL, O. PFANNKUCKE, P.J.D. LAMBSHEAD, A.J. GOODAY, T. FERRERO and A. DINET, 1994. Sampler bias in the quantitative study of deep-sea meiobenthos. *Mar. Ecol. Prog. Ser.*, **104** : 197-203.

BOUWMAN L.A., K. ROMEYN, D.R. KREMER and F.B. ES, 1984. Occurrence and feeding biology of some nematode species in estuarine aufwuchs communities. *Cah. Biol. Mar.*, **25** : 287-303.

BRUCE P.C., 1991. Resampling stats. Resampling Stats, Arlington, VA, 86.

BUSSAU C., 1993. Taxonomische und Ökologische Untersuchungen an Nematoden des Peru-Beckens. Ph. D. dissertation, Christian-Albrechts-Universität, Kiel, 621.

CULLEN D.J., 1973. Bioturbation of superficial marine sediments by interstitial meiobenthos. *Nature*, **242** : 323-324.

EFRON B. and G. GONG, 1983. A leisurely look at the bootstrap, the jackknife, and cross-validation. *Amer. Statist.*, **37** : 36-48.

FEGLEY S.R., 1987. Experimental variation of near-bottom current speeds and its effects on depth distribution of sand-living meiofauna. *Mar. Biol.*, **95** : 183-192.

GAGE J.D. and P.A. TYLER, 1991. Deep-Sea Biology. Cambridge University Press, Cambridge, 504.

GROSS T.F. and A.J. WILLIAMS III, 1991. Characterization of deep-sea storms. *Mar. Geol.* **99** : 281-302.

HEIP C., M. VINCX and G. VRANKEN, 1985. The ecology of marine nematodes. *Oceanogr. Mar. Biol. Ann. Rev.*, **23** : 399-489.

HESSLER R.R. and P.A. JUMARS, 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.*, **21** : 185-209.

HOLLISTER C.D. and A.R.M. NOWELL, 1991. HEBBLE epilog. *Mar. Geol.*, **99** : 445-460.

JENSEN P., 1979. Havbundens mikroskopiske dyreliv. In Danmarks Natur. Havet. Edited by A. Norrevang and J. Lundo, Politikens Forlag, Kobenhavn, 157-166.

JENSEN P., 1982. Diatom-feeding behaviour of the free-living marine nematode *Chromadorita tenuis*. *Nematol.*, **28** : 71-76.

JENSEN P., 1986. Nematode fauna in the sulphide-rich brine seep and adjacent bottoms of the East Flower Garden, NW Gulf of Mexico. IV. Ecological aspects. *Mar. Biol.*, **92** : 489-503.

JENSEN P., 1987. Feeding ecology of free-living aquatic nematodes. *Mar. Ecol. Prog. Ser.*, **35** : 187-196.

JENSEN P., 1988. Nematode assemblages in the deep-sea benthos of the Norwegian Sea. *Deep-Sea Res.*, **35** : 1173-1184.

JENSEN P., 1992. Predatory nematodes from the deep-sea : description of species from the Norwegian Sea, diversity of feeding types and geographical distribution. *Cah. Biol. Mar.*, **33** : 1-23.

JONGE V.N. De and L.A. BOUWMAN, 1977. A simple density separation technique for quantitative isolation of meiobenthos using the colloidal silica Ludox-TM. *Mar. Biol.*, **42** : 143-148.

JUMARS P.A., 1975. Environmental grain and polychaete species' diversity in a bathyal benthic community. *Mar. Biol.*, **30** : 253-266.

JUMARS P.A. and K. FAUCHALD, 1977. Between-community contrasts in successful polychaete feeding strategies. In Ecology of Marine Benthos. Edited by B.C. Coull, Univ. of South Carolina Press, Columbia, 1-20.

LAMBSHEAD P.J.D., 1993. Recent developments in marine benthic biodiversity research. *Oceanis*, **19** : 5-24.

LAMBSHEAD P.J.D. and M. HODDA, 1994. The impact of disturbance on measurements of variability in marine nematode populations. *Vie Milieu*, **44** : 21-27.

LAMBSHEAD P.J.D., B.J. ELCE, D. THISTLE, J.E. ECKMAN and P.R.O. BARNETT, In press. A comparison of the biodiversity of deep-sea marine nematodes from three stations in the Rockall Trough, Northeast Atlantic, and one station in the San Diego Trough, Northeast Pacific. Biodiversity Letters.

NEHRING S., 1992a. Die Vegetarier unter den freilebenden Nematoden. 1. Die Aufwuchsfresser. *Mikrokosmos*, **81** : 135-140.

NEHRING S., 1992b. Die Vegetarier unter den freilebenden Nematoden. 2. Die Depositfresser. *Mikrokosmos*, **81** : 260-266.

NEHRING S., 1993. Tube-dwelling meiofauna in marine sediments. *Int. Rev. Gesamten Hydrobiol.*, **78** : 521-534.

NEHRING S., P. JENSEN and S. LORENZEN, 1990. Tube-dwelling nematodes : tube construction and possible ecological effects on sediment-water interfaces. *Mar. Ecol. Prog. Ser.*, **64** : 123-128.

RICE A.L. and P.J.D. LAMBSHEAD, 1993. Patch dynamics in the deep-sea benthos : the role of a heterogeneous supply of organic matter. *In* Aquatic Ecology. Edited by P.S. Giller, A.G. Hildrew and D.G. Raffaelli, Blackwell Scientific Publications, Oxford, 469-497.

RICE A.L., M.H. THURSTON and B.J. BETT, 1994. The IOSDL DEEPSEAS program : introduction and photographic evidence for the presence and absence of a seasonal input of phytodetritus at contrasting

abyssal sites in the northeastern Atlantic. *Deep-Sea Res.*, **41** : 1305-1320.

RIEMANN F. 1974. On hemisessile nematodes with flagelliform tail living in marine soft bottoms and on micro-tubes found in deep sea sediments. *Mikrofauna Meeresbodens,* **40** : 1-15.

RIEMANN F. and M. SCHRAGE, 1978. The mucustrap hypothesis on feeding of aquatic nematodes and implications for biodegradation and sediment texture. *Oecologia,* **34** : 75-88.

ROMEYN K. and L.A. BOUWMAN, 1983. Food selection and consumption by estuarine nematodes. *Hydrobiol. Bull.*, **17** (2) : 103-109.

ROMEYN K., L.A. BOUWMAN and W. ADMIRAAL, 1983. Ecology and cultivation of the herbivorous brackish-water nematode *Eudiplogaster pararmatus. Mar. Ecol. Prog. Ser.*, **12** : 145-153.

RUTGERS VAN DER LOEFF M.M. and M.S.S. LAVALEYE, 1986. Sediments, fauna and the dispersal of radionuclides at the N.E. Atlantic dumpsite for low-level radioactive waste. Netherlands Institute for Sea Research, Texel, 134.

SOKAL R.R. and F.J. ROHLF, 1969. Biometry. W.H. Freeman and Co., San Francisco, 776 p.

THISTLE D., S.C. ERTMAN and K. FAUCHALD, 1991. The fauna of the HEBBLE site : patterns in standing stock and sediment-dynamic effects. *Mar. Geol.*, **99** : 413-422.

THISTLE D. and K.M. SHERMAN, 1985. The nematode fauna of a deep-sea site exposed to strong near-bottom currents. *Deep-Sea Res.*, **32** : 1077-1088.

THISTLE D., J.Y. YINGST and K. FAUCHALD, 1985. A deep-sea benthic community exposed to strong near-bottom currents on the Scotian Rise (Western Atlantic). *Mar. Geol.*, **66** : 91-112.

THURSTON M.H., B.J. BETt, A.L. RICE and P.A.B. JACKSON, 1994. Variations in the invertebrate abyssal megafauna in the North Atlantic Ocean. *Deep-Sea Res.*, **41** (9) : 1321-1348.

TIETJEN J.H., 1989. Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Abyssal Plain. *Deep Sea Res.*, **36** : 1579-1594.

TIETJEN J.H. and J.J. LEE, 1977. Feeding behavior of marine nematodes. In Ecology of marine benthos. Edited by B.C. Coull, Univ. South Carolina Press, Columbia, 21-35.

WEATHERLY G.L. and E.A. KELLEY Jr., 1982. « Too cold » bottom layers at the base of the Scotian Rise. *J. Mar. Res.*, **40** : 985-1012.

WIESER W., 1953. Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Verkommen bei freilebenden marinen Nematoden. *Ark. Zool. Ser.* II., **4** : 439-484.