

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

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Abstract. The abundances and biodiversity of nematode assemblages from two well studied bathyal sites, the Rockall Trough (three stations) and the San Diego Trough (one station), are compared in an attempt to associate patterns to ecological factors. The biodiversity of the nematode assemblages was found to be extremely similar in both locations, both in terms of community structure and the identifiable genera present, which is surprising in view of the differences in latitude, current speed and chemistry between the troughs, suggesting that these apparently important ecological factors were

not controlling agents for nematode diversity. Similarly, the bathymetric gradient across the Rockall Trough stations had no impact on biodiversity. Nematodes at San Diego Trough were found to be significantly less abundant than at the Rockall Trough and it is suggested that this may be the result of high macrofaunal activity in this region.

Key words. Marine nematodes, deep sea, bathyal, benthos, biodiversity, Rockall Trough, San Diego Trough.

INTRODUCTION

It has long been recognized that nematodes are one of the most abundant groups. Recently, it has been claimed that nematodes are one of the three major radiations in multi-celled organisms that have produced a large part of the world's species, the others being insects and fungi (Gaston, 1991).

Some 20,000 species are estimated to have been described (Platt & Warwick, 1983) of which about 4000 are free-living and marine. These figures seem low in comparison with the estimated number of insect species described (about 800,000—see Gaston, 1991 for a review), but the nematode figure is based on a much smaller 'sample' of the environment.

There have been few studies of deep-sea meio-

fauna. Since the pioneering work by Wigley & McIntyre (1964), abundance studies of the deep-sea meiobenthos have been reported from a little more than fifty stations in the Atlantic and, prior to Shirayama's (1984a,b) study of twelve stations from the Western Pacific, only four Pacific stations had been examined (Thiel, 1979). Jensen, Rumohr & Graf (1992) emphasized the importance of 'identifying the fauna (deep-sea nematodes) to the lowest possible taxon, i.e. species level'. Only ten studies have investigated deep-sea nematode diversity at the species level (Teitjen, 1976; Vitiello, 1976; Vivier, 1978; Dinert & Vivier, 1979; Tietjen, 1984; Thistle & Sherman, 1985; Hope in Spiess *et al.*, 1987; Jensen, 1988; Tietjen, 1989; Soetaert, Heip & Vinex, 1991). A rough calculation, therefore, suggests that nematode diversity from less than a square metre of sea bed has

been investigated in a deep-sea environment that covers slightly more than half the Earth's surface.

The objective of this study is to add to the limited knowledge available on the abundances and biodiversity of deep-sea nematodes and this study gives the first report on the community structure of free-living nematodes from a Pacific deep-sea site. This paper compares nematode abundances and biodiversity from two bathyal deep-sea environments—the Rockall Trough off the continental shelf of NW Europe and the San Diego Trough off the western continental shelf of North America. These two sites were chosen because their ecology is well-known, by deep-sea standards, giving a reasonable chance of relating differences in the patterns of nematode biodiversity and abundance to ecological factors.

Despite a superficial similarity (in depth and position off the western edge of a northern continent) the two troughs differ in latitude, hydrographic features and chemistry. Rockall is a well-oxygenated trough with moderately strong currents while San Diego Trough enjoys mild currents but is poorly oxygenated. In addition, there is a current-speed gradient down the Hebridean Terrace in the Rockall Trough.

MATERIALS AND METHODS

Description of localities

The Rockall Trough runs roughly northeast to southwest, bounded on the east by the continental shelf of the British Isles and on the west by the Rockall Bank. To the north is the Wyville Thomson Ridge and at the southern end the trough opens onto the Porcupine Abyssal Plain. The complex hydrography of the Rockall Trough was summarized by Ellet, Edwards & Bowers (1986).

The samples were taken from three sites on the Hebridean Terrace, at 545 m (56°23.8'N, 09°08.1'W), at 835 m (56°23.3'N, 09°16.5'W), and at 1474 m depth (56°32.4'N, 09°37.6'W), (Fig. 1). In general, there is a northerly current over this part of the trough. For example, at a station at 57°18.6'N, 9°40.4'W, Ellet & Huthnance (1984, unpublished CONSLEX Group Report) noted a mean current velocity of 6.13 cm s⁻¹, with a maximum of 25.70 cm s⁻¹, at mooring depths of 1562–1614 m (station depth 1640 m). Paterson (1993, his Fig. 6.18) and Paterson, Lambshead & Gage (in press) reworked the current-speed data from the CONSLEX report to demonstrate that a putative current impact declined down the Terrace. They

calculated the near bottom percentage of current speeds greater than 15 cm s⁻¹. At 500 m, it was 40%, declining to only 17% at 1500 m.

Gage (1979) noted that photographs from all locations surveyed in the Rockall Trough 'show evidence of current smoothing, and sometimes ripples' and therefore that 'it seems unlikely that the tranquil conditions usually thought typical of the abyssal environment exist anywhere in the Trough'.

Microscopic examination of the surface (1 cm) sediments from the three stations indicated that they were similar, *Globigerina* ooze intermixed with fine sand. Bottom-water salinity in this area is around 35.0 ppt and annual mean temperature is 5°C (Ellet & Martin, 1973).

The San Diego Trough is a basin adjacent to the coast of southern California. The sampling station was at 32°52.4'N, 117°45.5'W (Fig. 2) at a depth of 1050 m. In this area, the sea-floor is flat with biologically produced mounds, 5 cm high and 40 cm in diameter, and the sediment is a hemipelagic green mud (Thistle & Eckman, 1990). Current velocities are low, with a modal current at 100 cm above the bottom of 3 cm s⁻¹—maximum velocity 10 cm s⁻¹—(Thistle & Eckman, 1990). In comparison with the Rockall Trough, this is a low energy location.

The nearbottom waters in many of the bathyal basins off southern California have a low oxygen concentration; for example, that of Santa Catalina Basin is 15 µmol and that of San Clemente Basin is 60 µmol (Reimers, 1987). In these two basins, oxygen concentration often declines to zero in the upper 1 cm (Reimers *et al.*, 1986; Reimers, 1987; Archer *et al.*, 1989). Although no measurements of sediment oxygen concentrations have been made in San Diego Trough, the concentration of oxygen in its bottom water is similar to that of the neighbouring Santa Catalina and San Clemente Basins (Smith, 1974), so low oxygen concentrations in the top 1 cm of sediment may also occur in San Diego Trough.

Sampling methods

The Rockall Trough samples were taken with a multiple corer (Barnett, Watson & Connelly, 1984) from the RRS Challenger in April 1976 (Cruise No. 5B76). On recovery the samples were immediately fixed in 4% buffered formalin. The 0–1 cm layers from three cores were examined from each station: at 545 m 15/1 (i.e. drop 15, core 1), 15/2 and 15/4, at 835 m 13/1,

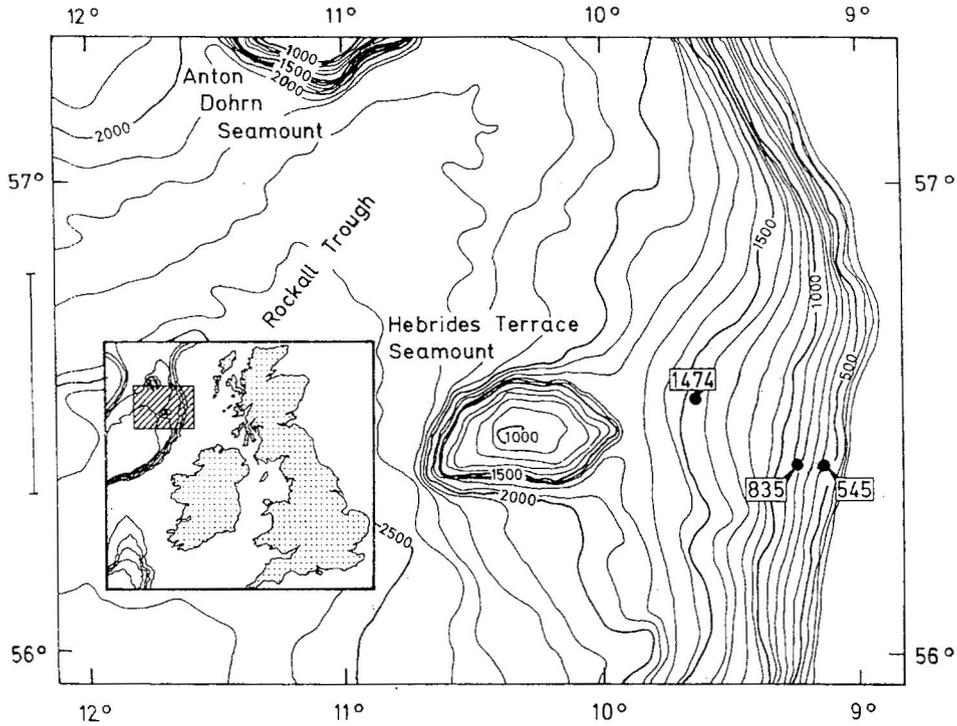


Fig. 1. Locations of the three stations in the Rockall Trough (contours in metres). Scale bar = 50 km.

13/2 and 13/3, and at 1474 m 6/1, 6/3 and 7/1. The nematodes were extracted by washing the samples on a 45 μm filter to remove the fine particles from the sediments and the worms were picked under a low-power microscope. The animals were too abundant to examine every specimen, so approximately 100 animals were subsampled at random from each core.

Six cores were used from the San Diego Trough in this study, labelled T3617, T3624, T3638, T3642, T3646, and T3648 (all from 1050 m). The samples were taken by the submersible D.S.V. Alvin, in 1987, using a 6.6 cm inner diameter corer from which a 0.9 cm diameter subcore had been removed for other purposes, leaving a sample area of 33.6 cm^2 for nematode analysis (Thistle & Eckman, 1990). On deck, the water overlying the core was drawn off through a 45 μm sieve. The top 1 cm of core was extruded and sliced off. The sieve and extrusion contents were immediately fixed in a sodium-borate buffered solution of 45 μmol filtered seawater and formalin (4:1 v/v). The nematodes were extracted as above. Nematode abundances were low at San Diego

Trough, so all specimens were mounted and identified.

Nematodes from the top 1 cm of sediment, only, were analysed.

Abundance

The nematodes were counted with a high-power microscope after they had been mounted. In the case of the Rockall samples, all the nematodes present in the cores were counted, not just the subsamples used in the taxonomic analysis.

Taxonomy

The nematodes were mounted in anhydrous glycerine on glass slides and examined under high-power, interference-contrast microscopy. The classification used in this paper is that of Platt & Warwick (1988), which is a slightly modified version of Lorenzen (1981). The specimens were sorted into nominal species using

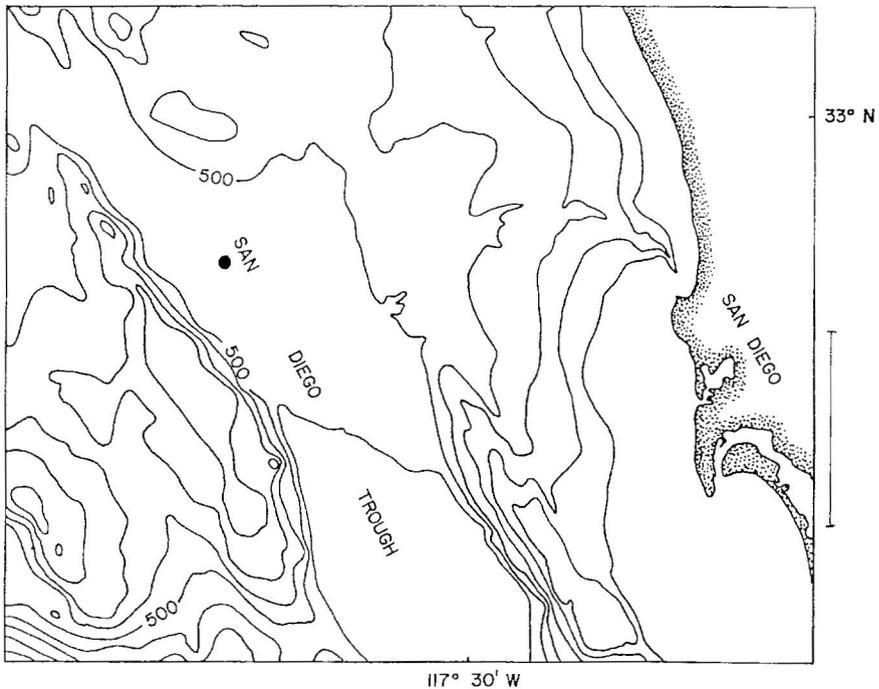


Fig. 2. Location of the station in San Diego Trough (contours in fathoms, 1 fathom = 1.83 m). Scale bar = 20 km.

morphological criteria. Most deep-sea nematode species are new to science and are often represented in the cores by very few individuals. The good male specimens that would be essential to check conspecificity of similar specimens from different stations are commonly lacking so nematodes were sorted independently for each station.

Diversity analysis

Diversity was analysed with two complementary methods; species richness (Sanders, 1968)—as measured by modified rarefaction curves (Hurlbert, 1971; Simberloff, 1972)—and Ewens–Caswell neutral model equitability analysis (Lamshead & Platt, 1988), calculated using logbase 'e' (Goldman & Lamshead, 1989). Full rarefaction curves have to be plotted to ensure that lines do not grossly cross, invalidating comparisons. Once this criterion is satisfied then a 'knot' can be chosen [$ES(X)$ —the expected number of species per abundance X] to standardize sample size and

allow valid statistical comparison of species richness.

The neutral model works by calculating the diversity of a theoretical sample, assuming no biological interactions or disturbance impact, which has exactly the same abundance and number of species as the 'real' sample under test. An equitability index, V , is calculated by subtracting the diversity of the 'theoretical' sample from the diversity of the 'real' sample and dividing by the standard deviation of the theoretical diversity.

Genera distribution analysis

The degree of taxonomic similarity between the samples from the Rockall and San Diego Trough stations was assessed by analysis of the genera present. The species level could not be used because of the difficulty in ensuring conspecificity between similar, undescribed specimens from different stations. However, a generic analysis should give a similar pattern to a species analysis but with some loss of resolution.

The analysis was undertaken using numerical cladistics. Cladistics creates groups according to the possession of shared characters, as opposed to overall similarity. The PAUP Wagner parsimony program was employed to obtain an unrooted tree (i.e. network). It was necessary to use an unrooted tree because more than one solution was possible with Lundberg Rooting, the preferred rooting method for this type of data (Lambshhead & Paterson, 1986). 'MINF' optimization with 'MULPARS' and 'global branch swapping' options were employed (Swofford, 1985).

The similarity between samples was also investigated using the non-metric, multidimensional scaling (MDS) option in the 'PRIMER Package' (Field, Clarke & Warwick, 1982). A similarity matrix was prepared using the Bray-Curtis similarity coefficient. A variety of data standardizations were employed (see Results).

RESULTS

Abundance

Abundances of nematodes in the Rockall Trough and San Diego Trough samples are given in Table 1. It is apparent that nematode abundances in the San Diego Trough station were lower than all the Rockall stations. The Rockall Trough Stations do not exactly match the depth of the San Diego Trough station but the 835 m and 1474 m stations straddle the latter's 1050 m depth. These two Rockall stations, when treated as a single station, show significantly more abundant nematodes than the San Diego station ($P = 0.0051$, NB Mann-Whitney test used for all probability testing). A more conservative test is to compare the deep 1474 m Rockall station with the 1050 m San Diego Trough samples. Choosing a deeper station makes the test conservative because nematode abundances would be expected to be lower there given the general decrease in abundance with depth (Sanders, Hessler & Hampson, 1965; Thistle, Vingst & Fauchald, 1985; Thistle, Ertman & Fauchald, 1991; Rex, Etter & Nimeskein, 1990; Tietjen, 1992). However, with only three points from the Rockall Trough the power of the test is low ($P = 0.028$). We conclude that the nematode abundances are significantly lower in the San Diego Trough samples.

Taxonomy

The 304 nematodes examined from the Rockall Trough station at 545 m were sorted into eighty nominal species. These species could be placed into fifty-four known genera (94.7%) and three genera apparently new to science. One of the fifty-four 'known genera' was described in an earlier phase of this project, *Bathyeurystomina valeriae* Lambshhead & Platt (1979), see Fig. 3. All the species could be placed within known families. The 292 nematodes examined from the 835 m station were sorted into eighty-three nominal species. Fifty-seven genera could be distinguished, fifty-three (93.0%) of which were known and four apparently new to science. All but four species (4.8%) could be placed in known families. The 334 nematodes examined from the 1474 m station could be sorted into ninety-three nominal species in fifty known genera (82.0%) and eleven genera apparently new to science. All species could be placed in thirty-four known families.

The 1355 nematodes from San Diego Trough were sorted into 116 nominal species, with thirteen individuals being unrecognizable ($> 0.01\%$) due to damage. Ninety-five of these species could be reasonably placed into sixty-four known genera (85.3%). Eight species could not be associated with any known genus

Table 1. Nematode abundances from the San Diego Trough and Rockall Trough samples

Sample	Depth (m)	Numbers per core	Numbers per 10 sq cm
San Diego Trough			
T3617	1050	245	72.9
T3624	1050	293	87.2
T3638	1050	160	47.6
T3642	1050	214	63.7
T3646	1050	312	92.9
T3648	1050	157	46.7
Rockall Trough			
15/1	545	564	225.0
15/2	545	926	383.7
15/4	545	912	363.7
13/1	835	448	178.7
13/2	835	752	300.0
13/3	835	1032	411.7
6/1	1474	574	229.0
6/3	1474	282	112.5
7/1	1474	391	156.0

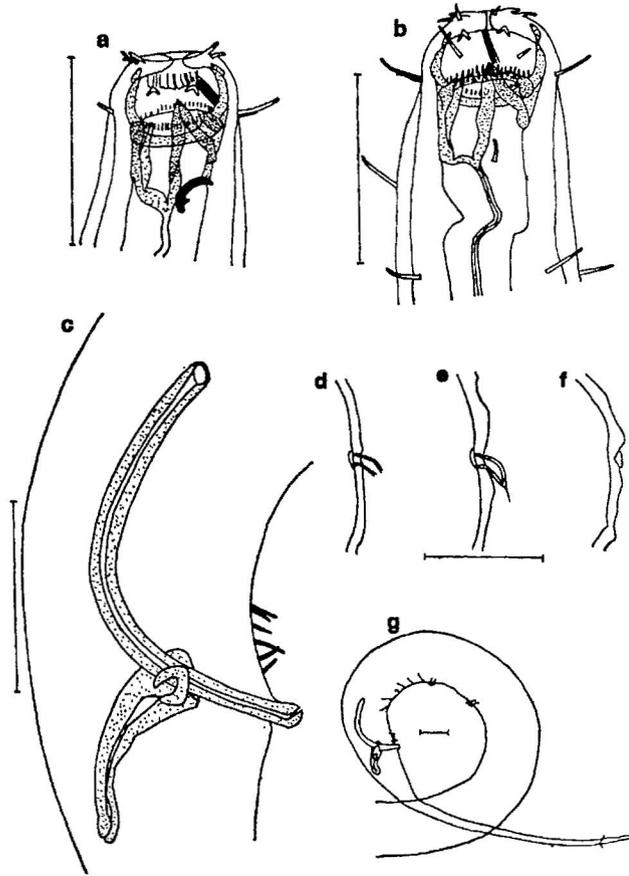


Fig. 3. A genus of free-living nematodes first described from the Rockall Trough (Lambshead & Platt, 1979). (a and b) Head of male and female respectively; (c, d, e and f) cuticularized male reproductive structures; and (g) male tail. Scale bar = 0.05 mm.

and three could not be reliably placed at the family level.

The composition of the nematode families from the two locations is shown in Table 2.

Diversity

The rarefaction plots (omitted here to save space as they convey no additional information) indicated that univariate comparison was valid (i.e. the curves did not cross), so ES(81) was used for analysis to compare the stations (Table 3); '81' individuals being the highest abundance 'knot' found in all samples. The San Diego Trough samples ES(81) estimates were not

significantly different from the pooled Rockall Trough samples ($P = 0.38$). Also, there was no change of species richness with depth in the Rockall Trough.

The V statistics for the samples are listed in Table 3. The San Diego Trough V statistics were not significantly different from the pooled Rockall Trough samples ($P = 0.52$), nor did equitability show any significant change with depth in the Rockall Trough.

Genera distribution analysis

Optimum parsimony yielded only one tree with a low consistency index of 0.52. Fig. 4 shows the structure of the unrooted tree. Each station grouped as a unit

Table 2. The composition of the nematode fauna by families (as percentages) in the stations by genera (G), Species (K) and specimens (S)

Family	San Diego Trough			Rockall 545 m			Rockall 835 m			Rockall 1474 m		
	G	K	S	G	K	S	G	K	S	G	K	S
Enoplidae	1.3	0.9	0.2	—	—	—	1.8	1.3	0.4	—	—	—
Thoracostomopsidae	2.6	1.8	0.2	—	—	—	1.8	1.3	0.4	—	—	—
Phanodermatidae	1.3	0.9	0.1	—	—	—	3.5	2.6	0.7	—	—	—
Oxystominidae	6.5	10.6	4.3	5.3	7.5	8.6	5.3	6.5	7.7	6.3	8.6	10.5
Oncholaimidae	1.3	0.9	0.2	1.8	3.8	2.3	3.5	2.6	2.1	—	—	—
Enchelidiidae	2.6	1.8	0.2	—	—	—	1.8	1.3	0.4	1.6	1.1	0.0
Tripyloididae	1.3	0.9	0.1	1.8	1.3	0.0	—	—	—	—	—	—
Trefusiidae	1.3	1.8	0.1	—	—	—	1.8	1.3	0.4	1.6	1.1	0.0
Chromadoridae	18.2	15.0	11.5	14.0	15.0	14.1	7.0	6.5	8.8	14.3	15.1	14.7
Comesomatidae	2.6	3.5	0.9	7.0	5.0	4.0	10.5	11.7	18.3	6.4	5.4	4.8
Ethmolaimidae	2.6	1.8	1.3	—	—	—	1.8	1.3	0.4	—	—	—
Cyatholaimidae	7.8	5.3	2.1	5.3	5.0	2.6	7.0	6.5	8.5	7.9	6.5	0.1
Selachinematidae	2.6	1.8	0.5	3.5	2.5	4.6	1.8	1.3	0.7	1.6	2.2	2.7
Desmodoridae	7.8	8.9	24.2	7.0	6.3	7.2	3.5	2.6	1.4	3.2	2.2	1.8
Draconematidae	1.3	0.9	0.9	—	—	—	—	—	—	—	—	—
Microlaimidae	2.6	6.2	8.0	3.5	7.5	27.0	1.8	7.8	14.8	3.2	4.3	8.4
Leptolaimidae	6.5	7.1	11.2	3.5	2.5	5.3	1.8	1.3	1.1	3.2	2.2	2.7
Aegialoalaimidae	1.3	0.9	0.2	—	—	—	3.5	2.6	0.7	3.2	3.2	1.8
Ceramoneematidae	3.9	5.3	14.0	7.0	7.5	3.0	3.5	3.9	4.2	1.6	1.1	1.5
Desmoscolecidae	5.2	4.4	8.2	5.3	8.8	8.2	5.3	5.2	5.3	11.1	9.7	14.4
Monhysteridae	1.3	0.9	0.5	1.8	1.3	0.0	1.8	2.6	1.4	3.2	8.6	6.6
Xyalidae	9.1	13.3	6.0	3.5	3.8	1.6	10.5	10.4	8.5	9.5	11.8	7.5
Sphaerolaimidae	2.6	1.8	0.3	—	—	—	3.5	2.6	1.4	3.2	4.3	10.5
Linhomoeidae	2.6	1.8	2.7	5.3	3.8	1.6	5.3	3.9	1.1	3.2	2.2	0.0
Diplopeltidae	3.9	2.7	2.9	7.0	5.0	2.0	5.3	7.8	4.6	3.2	2.2	0.0
Siphonolaimidae	—	—	—	3.5	2.5	0.0	—	—	—	1.6	1.1	0.0
Ironidae	—	—	—	1.8	1.3	0.0	1.8	1.3	5.6	3.2	2.2	1.5
Tubolaimoididae	—	—	—	1.8	2.5	0.0	1.8	1.3	0.4	3.2	2.2	0.0
Axonolaimidae	—	—	—	3.5	2.5	1.3	—	—	—	4.8	3.2	1.5
Pandolaimidae	—	—	—	1.8	1.3	2.0	—	—	—	—	—	—
Tarvaiidae	—	—	—	1.8	1.3	0.0	—	—	—	—	—	—
Anoplostomatidae	—	—	—	1.8	1.3	0.0	1.8	1.3	0.7	—	—	—
Coninckiidae	—	—	—	1.8	1.3	0.0	—	—	—	—	—	—
Meyliidae	—	—	—	—	—	—	1.8	1.3	0.4	—	—	—

Table 3. Diversity statistics of nematodes from the San Diego Trough and Rockall Trough. ES(81) = expected number of species for a sample of 81 individuals, V = Ewens-Caswell neutral model statistic.

Station	Sample	ES(81)	V
San Diego Trough	T3624	37.91	+ 0.66
	T3638	37.50	+ 0.02
	T3548	36.00	- 0.23
	T3617	31.35	- 1.82
	T3646	39.06	- 0.36
	T3642	35.20	- 0.91
Rockall 545 m	15/2	38.61	- 1.97
	15/1	37.54	+ 0.01
	15/4	38.88	- 2.17
Rockall 835 m	13/1	32.85	- 1.20
	13/2	41.52	- 0.59
	13/3	44.43	+ 0.74
Rockall 1474 m	6/3	34.43	+ 0.41
	7/1	34.45	- 0.44
	6/1	43.30	- 0.30

with Rockall 545 m station being most associated with San Diego Trough and Rockall 835 m station being most associated with Rockall 1474 m. There is, therefore, no evidence to suggest that the San Diego Trough station is more different from the Rockall stations in biodiversity, as indicated by the genera present, than the Rockall stations are from each other. Similarly, there is no evidence for a bathymetric effect over the depths tested (545–1474 m).

The different data manipulations for the MDS analysis had no important impact on the results. In Fig. 5 the data were standardized—as a percentage—to avoid problems of the San Diego samples being 'different' simply because they were larger than the Rockall subsamples and the data were transformed with square root (square root (x)). The plot was remarkably similar to the cladistic analysis. The four stations separated, but the Rockall 835 m and 1474 m stations were more closely associated than the other stations. Again there is no evidence to suggest that the San Diego Trough station is more different from the Rockall stations than they are from each other and there is little evidence for a bathymetric effect.

DISCUSSION

Taxonomy

The number of species recorded for the Rockall Sta-

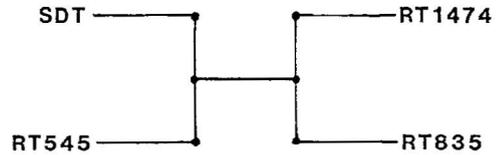


Fig. 4. Unrooted Wagner tree showing the relationship of the four stations using generic data. SDT = San Diego Trough, RT = Rockall Trough.

tions and for the San Diego Station are compared in Table 4 with other deep-sea studies. The numbers are slightly lower than the Caribbean and Mediterranean studies which analysed a similar number of animals and they are considerably lower than the previous Pacific study. It may be significant that the East Pacific Rise samples were abyssal (4500 m). Another possibility is that the sampling methodology in the East Pacific Rise study, a large number of very small subsamples (albeit from the same area) of ten or so specimens added together, might tend to increase measured species richness. Published figures often involve combining stations which raises measured species richness.

Most of the genera in this bathyal study were

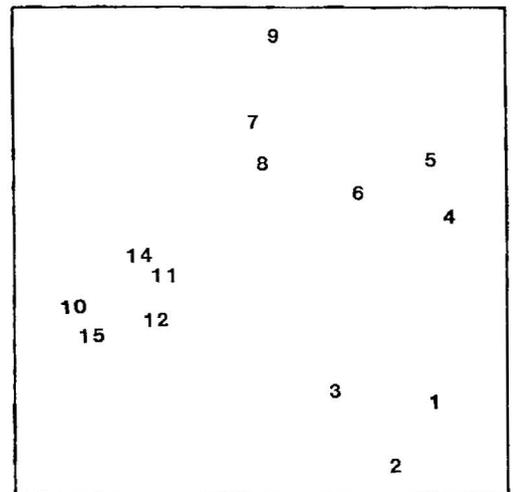


Fig. 5. Non-parametric multidimensional scaling ordination of the fifteen samples using generic data. Rockall Trough 545 m cores 15/2 = 1, 15/1 = 2, 15/4 = 3, 835 m cores 13/1 = 4, 13/2 = 5, 13/3 = 6, 1474 m cores 6/3 = 7, 7/1 = 8, 6/1 = 9, San Diego Trough cores T3624 = 10, 35 = 11, 48 = 12, 17 = 13, 46 = 14, 42 = 15. Note that 13 is obscured by 14.

Table 4. The number of species per number of individuals for ten deep-sea locations.

Location	Author	Depth (m)	No. of species	No. of specimens
San Diego Trough	This study	1050	116	1335
Rockall Trough		545	81	304
		835	83	292
		1474	93	334
Caribbean	Tietjen (1989)	2217–8380	227	1809
Norwegian Sea	Jensen (1988)	970–3294	92	?
East Pacific Rise	Hope (1987)	4500	148	216
HEBBLE	Thistle & Sherman (1985)	4626	205	2467
Venezuela Basin	Tietjen (1984)	3517–5045	136	1004
Bay of Biscay	Dinet & Vivier (1979)	1920–4725	316	14,000 +
Mediterranean	Vivier (1978)	300–580	212	1764
North Carolina	Tietjen (1976)	50–2500	96	?
Mediterranean	Vitiello (1976)	310–580	162	2000

known to science (82–95%). This is in contrast with Tietjen (1989) who found that only 51.8% of the genera of the Hatteras Plain (5411 m) and the Puerto Rico Trench (2217–8380 m) were known to science, but Tietjen also noted that 'Most of the unknown genera were represented by single or at most few specimens'. Our results are more similar to Hope in Spiess *et al.* (1987) who found 80.7% of the East Pacific Rise (4500 m) genera to be known to science. As most genera have been described from shallow water, the limited data would suggest that the dominant marine nematode genera have a global distribution at all depths.

Latitude

The lack of a nematode biodiversity difference associated with a 20° difference in latitude does not agree with the results obtained for deep-sea sediment dwelling macrofauna. Kendal & Aschan (1993) analysed three shallow sublittoral sites from 7°S to 78°N and concluded that the sites showed 'no real difference in diversity'. But Rex *et al.* (1993) showed a strong deep-sea macrofaunal latitudinal gradient in the North Atlantic, diversity declining as latitude increases.

Current speeds

The absence of any trend between species richness and equitability with either depth in the Rockall Trough or between the two troughs, is unexpected given that current energy declines with depth in the

Rockall Trough and that San Diego Trough enjoys low current disturbance. Paterson (1993) and Paterson *et al.* (in press) analysed polychaete diversity along the same depth gradient on the Hebridean Terrace as the Rockall stations here and found a significant increase in both species richness, as measured by $ES(X)$, and equitability, as measured by V . Paterson concluded that current energy was a controlling factor in bathyal polychaete diversity. The evidence here suggests that current energy has no influence on marine nematode diversity. This suggests that infaunal polychaete and infaunal nematode worms 'perceive' the environment quite differently.

Tietjen (1976) observed a significant decrease of nematode diversity with depth off North Carolina but he considered this to be caused by changes in sediment rather than current energy, and there appeared to be no important changes in sediment composition in the Rockall Trough stations. Soetaert *et al.* (1991) noted that 'Nematode diversity did not exhibit any clear correlation with station depth' over 160–1220 m in the Mediterranean. Dinet & Vivier (1979) reported an association between nematode diversity and depth in the north east Atlantic with a peak at 4000 m, a much greater range of depth than that studied here.

Abundance

Before the abundance results can be interpreted, it is necessary to consider whether the spread of abundances recorded here is within expected values or whether one or other of the two locations is unusual.

Table 5. Papers reporting nematode abundances, per 10 sq cm from 500 m to 2000 m depth—see text for explanation. Note that Dinet & Vivier's (1977) sample KR 13 was omitted as it appeared to be an outlier.

Author(s)	Depth (m)	Total nos	0–1 cm nos	Sampler
Coull <i>et al.</i> (1977)	800	437	188	Box corer
		604	260	
Dinet (1973)	1440		198	Box corer
			192	
			419	
Dinet & Vivier (1977)	1920	306	178	Box corer
	1913	451	262	
	1960	403	234	
	1957	748	434	
	1920	543	315	
	1960	435	252	
Pfannkuche (1985)	500	2382	1000	Multiple corer
	510	1676	704	
	960	1429	386	
	1492	820	295	
	2000	702	316	

It appears to be possible to predict approximate abundances of deep-sea infauna in at least two ways. Shirayama (1984a) used multiple regression to show that meiofaunal abundance in his data set from the North Pacific varies with several sediment parameters. Infaunal abundance also tends to decrease with increasing water depth and increasing distance from shore (see e.g. Sanders *et al.*, 1965; Thistle *et al.*, 1985; 1991; Rex *et al.*, 1990; Tietjen, 1992, review by Gage, 1991). Because of the shape of the ocean basins, water depth and distance from shore tend to covary, so by considering depth alone, it is possible to account for much of the variability in the flux of food to the seabed.

Table 5 shows comparable nematode abundance data from similar depths (500–2000 m). We included only data from studies that used box-corers or more efficient meiofauna samplers. Three of the studies that we used (Coull *et al.*, 1977; Dinet & Vivier, 1977; Pfannkuche, 1985) gave nematode abundances for sediment depths greater than the 0–1 cm layer used here, so these were adjusted proportionally, accepting of necessity that this involves adding a degree of error.

The results are displayed in Fig. 6. The Rockall samples are not unusually rich in nematodes but the San Diego Trough samples are conspicuously impoverished. So what factors could significantly reduce the nematode population levels in San Diego

Trough without affecting their biodiversity? Extreme physical disturbance can decrease nematode abundances, for example exposure in summer can affect littoral populations (Lamshead & Platt, 1988). But hydrodynamic effects can be eliminated as a causative agent in that Rockall is more energetic than San Diego Trough, which has a non-erosive nearbottom flow (Thistle & Eckman, 1990). Severe oligotrophic conditions can result in unusually low nematode abundances, for example in the Mediterranean (Eleftheriou, pers. comm.), or the Red Sea (Thiel *et al.*, 1987)—which is why Mediterranean or Red Sea data are not included in Fig. 6—but the San Diego Trough is not oligotrophic, as is indicated by the rich and abundant macrofauna found there (see below).

A possible explanation is the low oxygen concentrations in San Diego Trough. Shallow-water studies (e.g. Reise, 1981) have shown that nematode abundances can be reduced by low oxygen concentration. Environments controlled by physical factors strong enough to cause major reductions in populations, are predicted to have low ecological biodiversity (Platt & Lamshead, 1985; Lamshead & Platt, 1988), whatever model of community theory is employed (Sanders, 1968; Connell, 1978; Huston, 1979). Therefore, low oxygen levels sufficient to cause low nematode abundances in San Diego Trough should be reflected in the diversity statistics, but were not. In

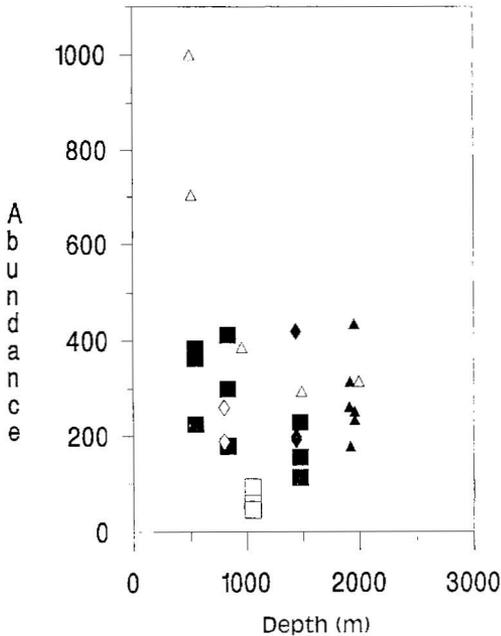


Fig. 6. A plot of nematode abundances of the top cm of sediment (per 10 cm²) from Table 1 and Table 5. Sample key as follows: ■, Rockall Trough; □, San Diego Trough; ◆, Dinet (1973); ◇, Coull *et al.* (1977); ▲, Dinet & Vivier (1977); △, Pfannkuche (1985).

addition, previous work on the San Diego Trough has found a rich fauna of copepods (Thistle & Eckman, 1990) and macrofauna (Jumars, 1978) which would also be difficult to reconcile with a major physical disturbance impact.

There is an additional way to test the low-oxygen hypothesis. Shallow water studies of low-oxygen nematode assemblages in the deeper sediment layers have suggested that there are specific species and genera associated with these assemblages (Fenchel & Riedl, 1970; Boaden & Platt, 1971; Powell *et al.*, 1983 and others—see references in Jensen, 1986). We could find no data on what deep-sea species might be associated with low oxygen sediments beyond the suggestion in Jensen *et al.* (1992) that the deep-sea species of the *Sabatieria pulchra* group may be physiologically adapted to low oxygen concentrations. In the 0–1 cm sediment samples from San Diego Trough there were no members of the genus *Sabatieria*. We also found no genera normally associated with oxygen poor systems (e.g. the genera of the Stilbonematinae, Jensen, 1986) in San Diego Trough.

We conclude that our data does not support the

suggestion that low oxygen levels are responsible for the unusually low abundances of nematodes in San Diego Trough.

It is, therefore, worth considering an alternative hypothesis, that macro- and mega-faunal activity is depressing nematode abundances. Previous work on the San Diego Trough has suggested that it is a biologically active environment and that the activities of macro- and mega-faunal organisms are an important factor in structuring the environment (Jumars, 1975; Thistle & Eckman, 1990). Certainly, the densities of larger organisms at San Diego Trough can be high. For example, adult ophiuroids are found at San Diego Trough at densities up to 33 m⁻² (Rokop, 1975) but at only 1 m⁻² on The Hebridean Terrace, Rockall Trough (Gage, unpublished data). Deep-sea macrobenthos are potential predators on the meiofauna (Tietjen, 1971). In shallow water, Tietjen (in Hanson *et al.*, 1981) noted that meiofauna biomass was inversely correlated with macrofaunal biomass. More specifically, Warwick *et al.* (1986) found that the feeding activity of the polychaete *Streblosoma bairdi* considerably reduced meiofauna abundance.

CONCLUSIONS

It is a sobering thought that the biodiversity patterns of the most abundant and diverse metazoan group in two highly studied deep-sea locations cannot be adequately associated with ecological processes. The stations in the two troughs are remarkably similar in marine nematode biodiversity in the top centimetre of sediment despite the latitude, current speed, chemical and macrofaunal-activity dissimilarities between these bathyal locations. Over the depth range studied, there was no bathymetric gradient of diversity. However, the San Diego Trough station displayed decreased nematode abundance. This phenomenon could not be related to any feature of the San Diego Trough but may be the product of high macrofaunal activity.

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