

# Free-living marine nematodes from hydrothermal sediments: similarities with communities from diverse reduced habitats

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**ABSTRACT:** The meiofauna of hydrothermal deep-sea sediments in the North Fiji Basin (NE Pacific) was investigated. Nematodes were the dominant taxon. The structure of the hydrothermal nematode communities from the Fiji Basin is compared with (1) the communities from adjacent oxic deep-sea sediments, (2) other hydrothermal vent areas and (3) shallow reduced environments such as cold seeps and subsurface anoxic sediments of eutrophic bottoms. Although the genus composition of the hydrothermal area and the biodiversity on a generic or functional-morphological level did not deviate greatly from the control areas, we found differences at the species level and in the size spectra and the species diversity. None of the species found in the hydrothermal sediments occurred in the surrounding areas. The size spectra of the vent communities was shifted towards larger nematodes, and species diversity was much lower in the hydrothermal area. The similarity in nematode genus composition between hydrothermal sites and control areas stands in contrast with the presence of a specialized endemic hydrothermal macrofauna. The absence of a planktonic life stage, in combination with small size, makes it more difficult for nematode species to migrate between isolated hydrothermal patches.

**KEY WORDS:** Nematodes · Hydrothermal vents · Community analysis · Colonization

## INTRODUCTION

Hydrothermal vents are extreme habitats, associated with tectonically active zones in the deep sea. The living conditions they provide are specialized, for 3 main reasons: high concentrations of reduced chemicals (mainly sulphide) maintain a chemo-autotrophic food chain; temperatures are high (more than 100°C in the centre); and the time scale of activity is limited (on the order of a decade). Additionally, hydrothermalism is limited to restricted areas of high tectonic activity, often less than 50 m wide, which makes them ephemeral, biogeographic islands. Discovered at the end of the 1970s, the mega- and macrofauna and the bacterial communities of these biotopes have been the subject of intensive investigation from the beginning (Grassle 1986). The intermediate-sized meiofauna, however, is only poorly known (Giere 1993).

During the HYFYFLUX cruise with the German research vessel FS 'SONNE' (cruise no. 99) (Auzende et al. 1995), meiofauna was sampled at the North Fiji Basin, a young back-arc basin located between the Tonga-Kermadec and New Hebrides subduction zones (Auzende et al. 1988). The first evidence of hydrothermal activity in the North Fiji Basin was provided by measurements of methane and manganese anomalies in water samples during the SEAPSO III cruise (Auzende et al. 1986). Since then, the geology and chemistry of active hydrothermal sites such as the White Lady, Père Lachaise and LHOS have been studied in more detail by Grimaud et al. (1991) and Bendel et al. (1993). Thus far only a brief description of the macrofauna of 2 active hydrothermal vent sites in the Fiji Basin has been published (Desbruyeres et al. 1994).

The aim of the present study is 3-fold. First, the structure of the meiofauna communities of hydrothermal sediments in the North Fiji Basin is investigated.

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The nematodes, as a dominant group within the meiofauna, are studied to species level. A distinction is made between sediments in the immediate vicinity of active vents, and sediments where geological and biological remains indicate recently terminated hydrothermal activity. Second, the hydrothermal meiofauna communities from the Fiji Basin are compared with those from adjacent deep-sea sediments outside the influence of recent hydrothermal activity. Finally, similarities between hydrothermal communities and the meiofauna from other reduced environments are evaluated. Apart from deep-sea hydrothermal vents, marine sediments become reduced in cold seeps, where gas, brine or oil seepage contaminates the soft bottoms. But reduction of the sediments is not only associated with geological activity. The microbial degradation processes in organically enriched sediments also leads to higher concentrations of dissolved hydrogen sulphide. All these extreme habitats have been found to harbour meiofaunal organisms, sometimes at high densities (Giere 1993). The composition of the nematode communities present in various reduced biotopes is reviewed, and their affinities are discussed in the context of some evolutionary aspects of the hydrothermal nematode fauna.

## MATERIAL AND METHODS

**Study area.** Hydrothermal sites along the central spreading ridge in the North Fiji Basin such as the White Lady, Père Lachaise and the LHOS site, are situated at 2000 m depth close to Vita Levu, the main island of the Fiji group (Fig. 1). The LHOS hydrothermally active site comprises a  $200 \times 200$  m composite vent field, with 5 more or less active vents and at least 4 wide patches of diffuse venting along an open fissure. The active vents are composed of anhydrite and expel shimmering water, whose maximum temperature was measured at 92.3°C during the STARMER cruise (Bendel et al. 1993).

**Field work.** During the first part of the SONNE 99 cruise (January 1995) large parts of the sea floor were explored by means of a photographic sledge (EXPLOS), on which a camera system was mounted to make direct observations of the sea floor. In this way the hydrothermally active sites were located. They were characterized by dense aggregations of large macrobenthic animals, in sharp contrast with the desolate surrounding sea floor covered by barren basalt rocks.

For selective, visually controlled spot-sampling of hard rocks, precipitates (soft sediments) and macrofaunal organisms, a Preussag TV grab (Type A) was used. The dimensions of this device with opened shovels are 1.3 m length, 2.0 m width and 2.7 m height.

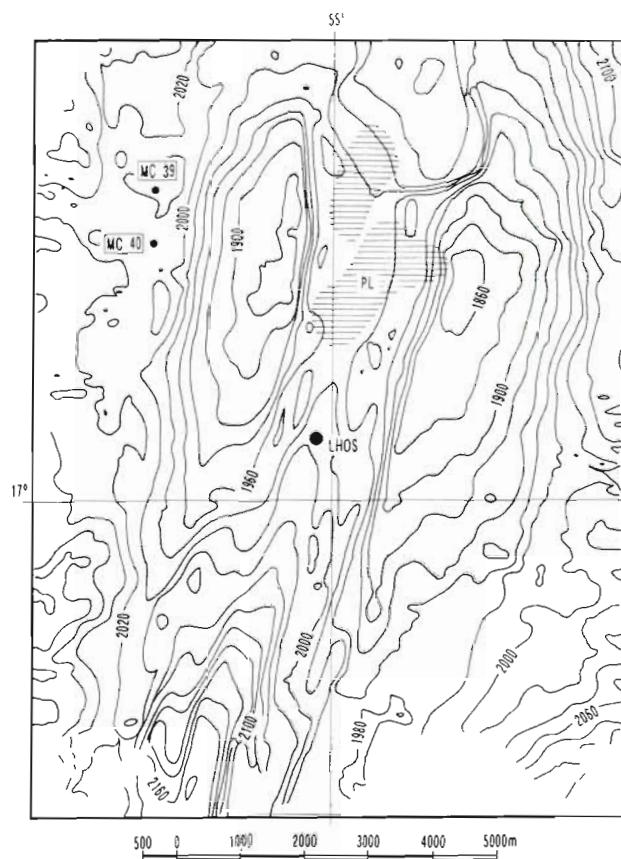


Fig. 1. Bathymetric map of the central ridge at the North Fiji back-arc basin, with the LHOS hydrothermal field and the deep-sea reference stations MC 39 and MC 40 shown (also shown is the Père Lachaise hydrothermal field, PL)

It can recover a sample volume of  $0.6 \text{ m}^3$ , and has a maximum penetration depth of 0.7 m. Soft bottoms, where hard substrates were lacking, were sampled by means of a multiple corer (MC; Barnett et al. 1984) which allowed quantitative, undisturbed sampling of the upper sediment layers.

Sediment for meiofaunal analysis was collected by means of the TV grab from different *Bathymodiolus* mussel fields at the LHOS area (= 'active hydrothermal sites'). The TV grab was also used to collect sediment from sites that were no longer active at the time of sampling, although geological and biological relics, such as old chimneys, basalts and aggregations of empty mollusc shells, indicated recent hydrothermal activity (= 'inactive hydrothermal sites'). Finally, quantitative MC samples were collected from soft bottoms situated at the same water depth, but without hydrothermal impact (= 'reference sites'). Table 1 shows the coordinates of all the sampling sites.

The sampling gear used at the hydrothermal sites did not allow an accurate chemical analysis. The presence of *Bathymodiolus* mussels and their dependence on sul-

Table 1. Coordinates and description of the sampling stations in the North Fiji Basin

Type	Stn	Date (1995)	Latitude	Longitude	Depth (m)	Description
Reference	MC 39	15 Jan	16° 57.41' S	173° 53.40' E	2033	Undisturbed sediment
	MC 40	16 Jan	16° 57.90' S	173° 53.28' E	2018	Undisturbed sediment
Hydrothermal active	GTV 91	22 Jan	16° 59.24' S	173° 55.00' E	1984	Basalt, sediment, mussels
	GTV 92	23 Jan	16° 59.47' S	173° 54.83' E	1988	Basalt, sediment, mussels
	GTV 98	24 Jan	16° 59.49' S	173° 54.83' E	1993	Basalt, sediment, mussels
Hydrothermal inactive	GTV 18	13 Jan	16° 57.50' S	173° 55.75' E	1915	Basalt, sediment
	GTV 21	13 Jan	16° 57.70' S	173° 55.57' E	1956	Basalt, sediment
	GTV 70	19 Jan	16° 59.39' S	173° 54.93' E	1984	Basalt, sediment
	GTV 97	23 Jan	16° 59.53' S	173° 54.91' E	1996	Basalt, sediment
	GTV 108	25 Jan	16° 57.48' S	173° 54.98' E	1967	Basalt, sediment

phide (Nelson et al. 1995), together with the visual observation of sulphides on board immediately after collection, provide the main evidence for a hydrothermal impact on the collected nematode communities.

Three deployments of the TV grab (GTV 91, GTV 92 and GTV 98) contained considerable amounts of sediment and hydrothermal macrofauna (e.g. *Bathymodiolus* sp., *Ifremeria nautili*). On board the sediment was sampled carefully from in between the basalt rocks with a spatula. Because these samples were not collected with a core they were expressed as a volume (cm<sup>3</sup> sediment).

Five deployments of the TV grab at the formerly active sites on the central ridge (GTV 18, 21, 70, 97, 108) contained sediment together with basalt rocks. No live macrobenthic fauna were present, but occasionally empty gastropod and mussel shells were observed in high densities. These GTV deployments were spread over the area and are considered as replicates of the inactive hydrothermal sediments.

On the western flank of the Central Fiji ridge at a depth of 2030 m, sediment was collected quantitatively. The absence of basalt rocks allowed core samples of the soft bottom-sediments to be taken. Replicate deployments of the multiple corer, MC 39 and MC 40 (25.52 cm<sup>2</sup> surface area and 4 cm depth), were made to characterize deep-sea sediments outside the influence of recent hydrothermal activity.

**Sample processing and evaluation.** Immediately after sampling, the sediment samples were fixed with a neutralized formaldehyde solution to a final concentration of 4%. The meiofauna was extracted from the sediment by centrifugation with Ludox (see Heip et al. 1985) using a 32 µm sieve. The metazoan meiofauna was counted for each sample, and all nematodes were picked out and mounted on slides. Nematode biomass was estimated by Andrassy's (1956) formulae based on length and width measurements of individuals. Size spectra were constructed using geometric size classes in which class 0 = 0.00465 to 0.0093 µg dry wt, class 1 = 0.0093 to 0.0186 µg dry wt and so on (Warwick 1984).

Nematodes were identified to genus level, and for each genus, species were distinguished and compared between samples. All dominant species are new to science and will be described at a later stage of the investigation.

Diversity indices were calculated as suggested by Heip et al. (1988) using the Hill's diversity numbers of order 1 ( $N_1$ : the exponential of the Shannon Wiener index  $\times \ln 2$ ), 2 ( $N_2$ : the reciprocal of Simpson's evenness index) and infinity ( $N_{\infty}$ : the reciprocal of the abundance of the most common species).  $H'$  is the Shannon Wiener diversity index [ $H' = -\sum p_i \cdot (\log p_i)$ , where  $p_i$  is the proportional abundance of species  $i$  in the sample].

Affinities between samples were analyzed by the multivariate technique of Correspondence Analysis (CA; Jongman et al. 1987, Ter Braak 1989) after an arcsine transformation of the relative abundances of genera (Sokal & Rohlf 1981). CA is a direct ordination method that arranges sites along axes on the basis of taxa-composition data.

A 1 ml subsample of each homogenized sample was processed with a Coulter counter to determine the silt fraction (<63 µm) and the median grain size of the 0.4 to 900 µm fraction.

## RESULTS

### Environmental factors

GTV 98 contained the highest portion of hydrothermal macrofauna (more than 20 *Bathymodiolus* specimens), indicating a strong hydrothermal influence. At Stns GTV 91 and GTV 92 only a couple of *Bathymodiolus* specimens were present, suggesting that these sites were located at the margins of the active hydrothermal spots.

The sediments at both hydrothermal and reference stations were very similar: very fine sand (median of 82 to 85 µm) with 35 % silt.

### Meiofauna composition and densities

Active hydrothermal sediments contain up to 1500 nematodes per 150 cm<sup>3</sup> of sediment (Table 2). Other meiofaunal taxa were scarce: up to 16 harpacticoids, 7 turbellarians, 5 bivalves, 3 polychaetes, 2 oligochaetes, 1 kinorhynch and 1 amphipod per 150 cm<sup>3</sup> sediment. Although nematodes always occurred in high abundances, their distribution was patchy. Three subsamples, two of 150 cm<sup>3</sup> and one of 450 cm<sup>3</sup>, randomly collected from the GTV 91 grab contained, respectively, 1265, 1500 and 116 ind. 150cm<sup>-3</sup>. The GTV 92 grab contained only 38 nematodes 150cm<sup>-3</sup>. In GTV 98, 487 nematodes were present per 150 cm<sup>3</sup> of sediment, together with 16 harpacticoids, 3 turbellarians and 2 polychaetes.

In the inactive ridge sediments, devoid of macrofaunal organisms, the abundance of meiofaunal taxa never exceeded 76 ind. 150cm<sup>-3</sup> sediment (Table 3). Nematodes amounted to a maximum of 64 ind. 150cm<sup>-3</sup>. For harpacticoids and polychaetes 6 ind. 150cm<sup>-3</sup> and for oligochaetes 2 ind. 150cm<sup>-3</sup> sediment were the maximum found. In addition, the meiofauna was patchy: subsamples from the same grab contained between 4 and 76 individuals. In some subsamples meiofauna was completely absent.

Table 2. Meiofauna densities (no. of individuals per volume) in active hydrothermal sediments of the North Fiji Basin

Subsample volume:	GTV 91			Sum 750 cm <sup>3</sup>	GTV 92 150 cm <sup>3</sup>	GTV 98 150 cm <sup>3</sup>
	150 cm <sup>3</sup>	150 cm <sup>3</sup>	450 cm <sup>3</sup>			
Nematoda	1500	1265	348	3113	38	487
Harpacticoidea	4	12	8	24		16
Turbellaria		7	3	10	3	3
Bivalvia		5	3	8		
Polychaeta		3	2	5	1	2
Oligochaeta		1	1	2	2	
Amphipoda			1	1		
Kinorhyncha		1		1		
Nauplii		1		1		
Sum	1504	1295	366	3165	44	508

Table 4. Meiofauna densities (mean no. of individuals per 25.52 cm<sup>2</sup>) at the reference deep-sea stations MC 39 and MC 40. (The volume of the total core is 100 cm<sup>3</sup>)

	MC 39	MC 40
Nematoda	871	812
Harpacticoidea	32	42
Nauplii	15	9
Polychaeta	11	12
Oligochaeta		2
Turbellaria	3	4
Tantulocarida	2	
Kinorhyncha	2	1
Ostracoda	1	2
Tanaidacea	1	
Bivalvia	1	2
Sipunculida	1	
Gastrotricha		1
Gastropoda		1
Amphipoda		1
Sum	940	889

In the reference deep-sea sediments, meiofaunal densities were 889 to 940 ind. 100cm<sup>-3</sup> (= 1334 to 1409 ind. 150cm<sup>-3</sup>) (Table 4). Nematodes dominated (more than 90%), followed by harpacticoids (4.7%). Other taxa occurring at both stations in abundances lower than 2.5% were Polychaeta, Turbellaria, Kinorhyncha, Ostracoda and Bivalvia.

### Composition of the nematode communities

The nematode fauna present in sediments that are geochemically affected by hydrothermal activity is not specialized at the generic level: thus far all specimens investigated from geographically distinct sites have belonged to genera known to science. In some cases poor preservation prevented identification to the genus level.

Table 3. Meiofauna densities in inactive hydrothermal sediments of the North Fiji Basin

Subsample volume:	GTV 18				Sum 600 cm <sup>3</sup>	GTV 21			Sum 450 cm <sup>3</sup>	GTV 70	GTV 97	GTV 108
	150 cm <sup>3</sup>	150 cm <sup>3</sup>	150 cm <sup>3</sup>	150 cm <sup>3</sup>		150 cm <sup>3</sup>	150 cm <sup>3</sup>	150 cm <sup>3</sup>		150 cm <sup>3</sup>	150 cm <sup>3</sup>	150 cm <sup>3</sup>
Nematoda	37	4	9	64	114			2	2	26	7	4
Harpacticoidea	6		1	4	11					3	2	
Polychaeta	4		3	6	13					3		
Oligochaeta	2			2	4							
Sum	49	4	13	76	142	0	0	2	2	32	9	4



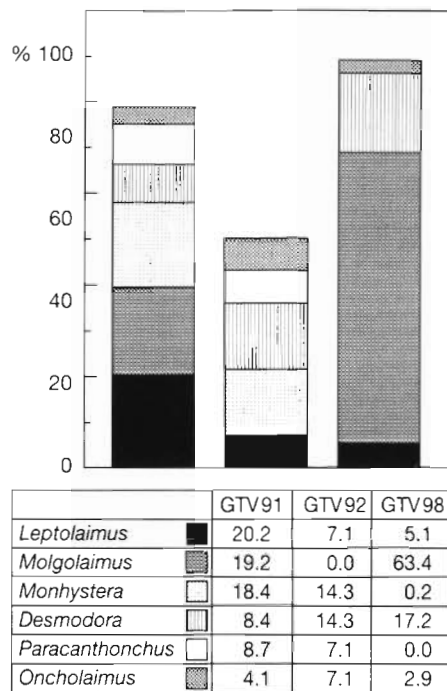


Fig. 2. Relative abundances of the dominant genera in sediments from active hydrothermal sites of the North Fiji Basin

In the GTV 91 grab 3113 nematodes were found and more than 80% of the community was made up of 6 genera (Fig. 2, Table 5). The genera *Leptolaimus* (20.2%), *Molgolaimus* (19.2%), and *Monhystera* (18.4%)

were dominant. *Paracanthionchus* (8.7%), *Desmodora* (8.4%) and *Oncholaimus* (4.1%) were subdominant genera. Although the sediment of the GTV 91 grab was collected haphazardly between the grabbed basalt and macrofauna, and subdivided into 3 subsamples, all subsamples contained a rather similar generic composition and dominance. The 2 most abundant genera among the nematodes collected at the GTV 92 station were *Desmodora* and *Monhystera*, each contributing 14.3%. In addition, *Leptolaimus*, *Paracanthionchus* and *Oncholaimus* each represented 7.1% of the nematodes (Fig. 2, Table 5). However, other genera were also important, such as *Acantholaimus* and *Marylinnia*, both at 10.7%, and *Syringolaimus* at 7.1%. The community of the most central hydrothermal site (GTV 98) contained 63% *Molgolaimus*, 17% *Desmodora*, with *Leptolaimus* and *Oncholaimus* contributing only 5.1 and 2.9% respectively (Table 5).

At the hydrothermal inactive ridge sites, nematodes were rather scarce with densities varying from 2 to 51 ind. 100cm<sup>-3</sup> of sediment. *Monhystera* dominated all the samples except for GTV 97. Other genera frequently found were *Daptonema*, *Acantholaimus* and *Leptolaimus*. Since the densities were very low and the samples not quantitatively collected, these data were handled below with caution.

Both soft bottom samples (MC 39 and MC 40; Table 6) were characterized by the same dominant genera: *Monhystera* (34%) and *Acantholaimus* (10%). Subdominant genera with an abundance of 2% or more

Table 5. Dominant genera ( $\geq 0.1\%$ ) of the hydrothermal sediments of the North Fiji Basin

GTV 91		GTV 92		GTV 98	
Genus	%	Genus	%	Genus	%
<i>Leptolaimus</i>	20.2	<i>Monhystera</i>	14.3	<i>Molgolaimus</i>	63.4
<i>Molgolaimus</i>	19.2	<i>Desmodora</i>	14.3	<i>Desmodora</i>	17.2
<i>Monhystera</i>	18.4	<i>Marylinnia</i>	10.7	<i>Leptolaimus</i>	5.1
<i>Paracanthionchus</i>	8.7	<i>Acantholaimus</i>	10.7	<i>Oncholaimus</i>	2.9
<i>Desmodora</i>	8.4	<i>Oncholaimus</i>	7.1	<i>Microlaimus</i>	1.6
<i>Oncholaimus</i>	4.1	<i>Syringolaimus</i>	7.1	<i>Symplocostoma</i>	0.6
<i>Paralinhomoeus</i>	3.7	<i>Paracanthionchus</i>	7.1	<i>Marylinnia</i>	0.6
<i>Actinonema</i>	2.4	<i>Leptolaimus</i>	7.1	<i>Paralinhomoeus</i>	0.2
<i>Daptonema</i>	2.4	<i>Prochromadorella</i>	3.6	<i>Daptonema</i>	0.2
<i>Calomicrolaimus</i>	2.0	<i>Southerniella</i>	3.6	<i>Monhystera</i>	0.2
<i>Acantholaimus</i>	1.1	<i>Terschellingia</i>	3.6	<i>Southerniella</i>	0.2
<i>Marylinnia</i>	1.0	<i>Wieseria</i>	3.6	<i>Cephalanticoma</i>	0.2
<i>Microlaimus</i>	0.9			<i>Anticoma</i>	0.2
<i>Halalaimus</i>	0.4				
<i>Syringolaimus</i>	0.4				
<i>Prochromadora</i>	0.2				
<i>Aegialoalaimus</i>	0.2				
<i>Southerniella</i>	0.1				
<i>Innocuanema</i>	0.1				
<i>Diplopeltula</i>	0.1				
<i>Chromadorina</i>	0.1				
<i>Axonolaimus</i>	0.1				
<i>Euchromadora</i>	0.1				
<i>Sphaerolaimus</i>	0.1				

Table 6. Genus composition (%) of the nematode communities in the reference deep-sea sediments of the North Fiji Basin

	MC 39	MC 40	Mean
<i>Monhystera</i>	34.4	33.8	34.1
<i>Acantholaimus</i>	10.7	9.7	10.2
<i>Daptonema</i>	6.7	2.1	4.4
<i>Diplopeltula</i>	3.0	3.4	3.2
<i>Halalaimus</i>	1.0	3.9	2.5
<i>Leptolaimus</i>	3.4	1.4	2.4
<i>Manganonema</i>	2.3	2.5	2.4
<i>Microlaimus</i>	2.1	2.1	2.1
<i>Bolbolaimus</i>	0.9	2.3	1.6
<i>Desmodora</i>	1.2	1.8	1.5
<i>Paracanthochus</i>	0.9	2.1	1.5
<i>Aegialolaimus</i>	2.0	0.7	1.4
<i>Metadasynemoides</i>	1.0	1.5	1.2
<i>Southerniella</i>	1.5	0.9	1.2
<i>Camacoolaimus</i>	1.3	1.0	1.2
<i>Gerlachius</i>	2.0		1.0
<i>Campylaimus</i>	1.4	0.5	0.9
<i>Syringolaimus</i>	0.6	1.1	0.9
<i>Molgolaimus</i>	0.9	0.8	0.9
<i>Calomicrolaimus</i>	0.3	1.3	0.8
<i>Ceramonema</i>	0.1	1.5	0.8
<i>Desmoscolex</i>	0.2	1.2	0.7
<i>Litinium</i>	0.9	0.5	0.7
<i>Actinonema</i>	0.1	1.1	0.6
<i>Metacyatholaimus</i>	1.1		0.5
<i>Eudraconema</i>	0.1	0.8	0.5
<i>Marylynna</i>	0.9		0.4
<i>Tricoma</i>	0.3	0.5	0.4
<i>Cervonema</i>	0.1	0.7	0.4
<i>Metadesmolaimus</i>		0.7	0.3
<i>Oncholaimus</i>		0.5	0.2
<i>Omicronema</i>	0.3	0.1	0.2
<i>Leptolaimoides</i>	0.2	0.2	0.2
<i>Disconema</i>	0.2	0.2	0.2
<i>Oxystomina</i>		0.3	0.2
<i>Meylia</i>		0.3	0.2
<i>Diplopeltoides</i>		0.2	0.1
<i>Thalassoalaimus</i>	0.1	0.1	0.1
<i>Cephalanticoma</i>	0.1	0.1	0.1
<i>Trichotheristus</i>		0.2	0.1
<i>Metalinhomoeus</i>		0.2	0.1
<i>Araeolaimus</i>		0.2	0.1
<i>Paramonhystera</i>		0.2	0.1
<i>Anaplostoma</i>		0.2	0.1
<i>Leptosomatium</i>		0.2	0.1
<i>Euchromadora</i>		0.2	0.1
<i>Quadricoma</i>		0.2	0.1
Desmoscolecidae	3.7	1.8	2.8
Cyatholaimidae		0.8	0.4
Desmodoridae		0.5	0.2
Leptolaimidae	0.2	0.2	0.2
Enoplida		0.3	0.2
Chromadoridae		0.3	0.2
Xyalidae		0.3	0.2
Unidentified	12.7	12.7	12.7

and present in both samples were *Diplopeltula* (3%), *Manganonema* (Bussau 1993) (2.5%) and *Daptonema* (from 2 to 7 %).

In the hydrothermal area (GTV 91, 92 and 98), the species/genus ratio was 1 except in the case of *Leptolaimus* and *Monhystera*. In the GTV 91 sample, *Leptolaimus* was represented by 2 species, of which *Leptolaimus* sp. 1 was most abundant (17.2% of the total community), compared to *Leptolaimus* sp. 2 (3%). The genus *Monhystera* was represented by 2 species: *Monhystera* sp. 1 was dominant (18.8%), while *Monhystera* sp. 2 was rarely found (Fig. 3B).

The soft bottom samples, MC 39 and MC 40, were characterized by a very high species/genus ratio for most of the dominant genera: *Monhystera* was represented by 11 species (Fig. 3A), *Acantholaimus* by as many as 14 species, *Halalaimus* and *Diplopeltula* each by 8 species, *Microlaimus* by 4 species, *Daptonema* by 7 species, *Manganonema* and *Metadasynemella* both by 3 species and *Paracanthochus*, *Desmodora*, *Ceramonema* and *Calomicrolaimus* each by 2 species.

Although several genera including some dominant ones such as *Monhystera*, *Leptolaimus*, *Acantholaimus* and *Molgolaimus* are common for both hydrothermal and reference sediments, none of the species present in the reference samples were found in the hydrothermal sediments. Fig. 3 illustrates the total diversity observed within the genus *Monhystera* at the hydrothermal and the reference sites. Also, the species observed at the inactive hydrothermal sites differed from those at the active sites.

### Biodiversity

Several biodiversity indices were calculated for GTV 91 and GTV 98 as representatives of the active hydrothermal sediments, and for the 2 MC samples containing soft deep-sea sediments (Table 7). In both types of samples all individuals were identified. At the generic level, biodiversity indices such as  $N_2$ ,  $N_{+∞}$  and  $H'$  were very similar for both deep-sea and hydrothermal sediments. However, at the species level the differences become more pronounced: the high species diversity both in number of species and dominance in the deep-sea sediment samples was in sharp contrast to the low diversity in the hydrothermal area.

### Size spectra

Body size measurements and weight estimates from both the hydrothermal GTV samples and the MC samples illustrate that on average, nematodes present in the hydrothermal sediments were twice as large as those in the reference sediments (Table 8). The size spectra illustrate that the smallest nematodes were absent in the hydrothermal sediments (Fig. 4).

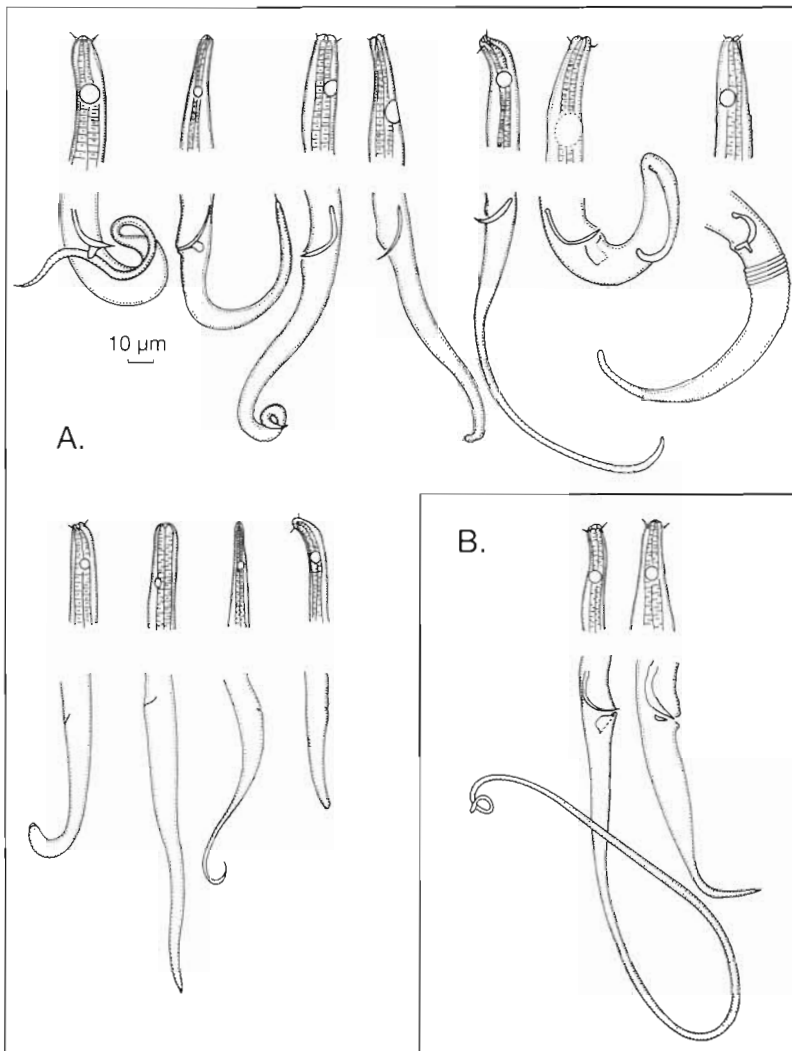


Fig. 3. Head and tail region of the morphospecies distinguished within the genus *Monhystera* (A) from the reference sediments and (B) from the active hydrothermal sediments. (If present, a male is shown. The other cases always show a juvenile)

## DISCUSSION

### Composition of the nematode communities: comparison with other hydrothermal sites

While physiological, ecological, biogeographical and evolutionary aspects of the hydrothermal macrofaunal and bacterial species associations have been intensively investigated since their discovery, the nematodes from these habitats are hardly known (Grassle 1986, Hessler et al. 1988, Gage & Tyler 1991, Tunnicliffe & Fowler 1996). It is mainly the constitution of the substrate at hydrothermal vents that has hampered the investigation of meiofauna, including the nematodes. The sediments do not cover the underlying basalt rocks sufficiently to allow the use of standard meiobenthological sampling devices (coring). So far meiofaunal analyses have been limited to the sediment-dwelling nematodes from small amounts of hydrothermal sediment (Dinet et al. 1988, Shirayama 1992). The present study in the North Fiji Basin faced similar sampling problems. As a result, only 1 l of hydrothermal soft substrate was collected, yielding a total of 3600 nematodes.

The black sediments from the *Bathymodiolus* fields are characterized by the overall dominance of nematodes. The high abundance of nematodes is in accordance with previous observations by Dinet et al. (1988) on the East Pacific

Table 7. Hill's diversity numbers and the Shannon Wiener index at the species and genus level at the hydrothermal and reference stations

Stn	$N_1$	$N_2$	$N_{\text{genus}}$	$H'$
<b>Genus</b>				
GTV 98	3.6	2.2	1.5	1.8
GTV 91	8.9	6.3	4.1	3.2
MC 39	11.7	5.4	2.6	3.5
MC 40	15.0	5.9	2.6	3.9
<b>Species</b>				
GTV 91	10.6	7.4	4.8	3.4
MC 40	63.3	37.0	10.5	6.0

Table 8. Mean nematode sizes in the North Fiji Basin

	MC 40	MC 39	GTV 18, 21, 97, 108	GTV 91	GTV 98
<b>Length (µm)</b>					
Arithmetic	515.28	444.63	588.54	812.45	804.16
SD	407.63	255.27	385.91	542.34	293.52
Geometric	442.87	398.81	513.04	722.96	779.77
<b>Width (µm)</b>					
Arithmetic	16.09	13.56	15.08	18.36	20.10
SD	8.27	6.76	7.36	9.37	3.10
Geometric	14.51	12.42	13.79	16.49	19.93
<b>Weight (µg wet wt)</b>					
Arithmetic	0.169	0.094	0.155	0.345	0.229
SD	0.733	0.360	0.377	1.079	0.326
Geometric	0.058	0.038	0.061	0.123	0.184

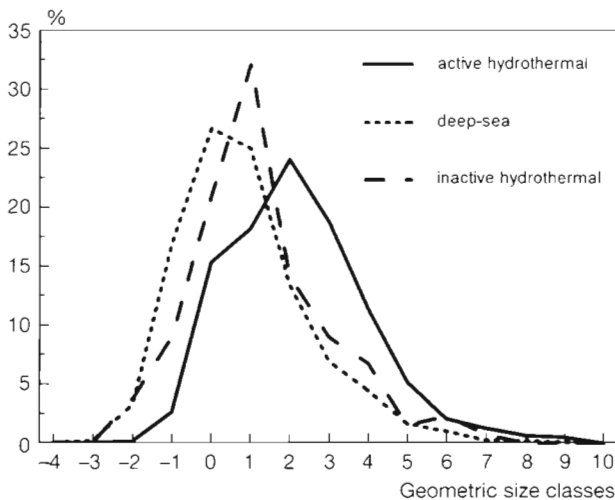


Fig. 4. Size distribution of nematodes in the North Fiji Basin

ridge and by Shirayama (1992) on the Iheya ridge. Only the second study produced a detailed species list, but it was based on 138 nematodes in the single sample collected. Comparison with the results of Diné et al. (1988) is even more inconclusive. The authors identified the nematodes present only to family level. Moreover they refer to the Epsilonematidae as one of the subdominant groups, but the corresponding illustration clearly shows a specimen of the genus *Desmodora* (Verschelde et al. in press). The overall dominance of the Microlaimidae on the East Pacific ridge (Diné et al. 1988) is not in accordance with observations at the North Fiji Basin, unless the authors classified *Molgo-laimus* as a microlaimide. *Molgo-laimus*, the dominant genus at the hydrothermal sites of the North Fiji Basin, is very similar in its external morphology to the Microlaimidae. This genus was erected by Jensen in 1978 from the Microlaimidae on the basis of the presence of a single anterior testis and reflexed ovaries, and placed within the Molgo-laimidae.

Four species (and genera) represent 85% of the community in the Iheya sample (Shirayama 1992). Two of these genera are also abundant in the North Fiji Basin: the genus *Leptolaimus* and a genus from the Monhysteridae group. However, the 2 other dominant genera were not found in the Fiji Basin: *Neochromadora* (44%) and *Desmolaimus* (24%). Species diversity definitely decreases from the soft deep-sea floor without hydrothermal influence to the active sites on the central Fiji ridge. None of the species are common to both habitats, but most of the dominant genera at the hydrothermal sites are represented, although with low abundances, in the unaffected deep-sea sediments. Only the high abundance of the genus *Monhystera* in the reference deep-sea samples from the Fiji Basin (37%) is similar to the hydrothermal sediments (up to 21%). In the hydro-

thermal sediments more than 80% of the community is made up by 5 species. In the adjacent deep-sea sediments less than 25% of the community is represented by the 5 most abundant species. Shirayama (1992) and Diné et al. (1988) also observed a low diversity in comparison to other deep-sea nematode communities at similar depths. According to Diné et al. (1988), their most remarkable observation is the inverse relationship between biodiversity and the concentration of hydrogen sulphide. The lower diversity and higher dominance of *Molgo-laimus* at the center of the hydrothermal site (GTV 98) in comparison to the margins (GTV 91) at the central Fiji ridge confirm this assessment.

#### Composition of the nematode communities: comparison with other reduced sites

Because of the low number of investigations on nematodes from hydrothermal sites, the nematode communities observed at the Fiji Basin were compared with those from other habitats characterized by similar biochemical living conditions. Indeed, marine sediments are not only reduced due to hydrothermal activity. Cold seepage of methane, brine, oil or ammonium also generates a sulphidic environment where macro- and microbenthic organisms display similar ecophysiological adaptations (e.g. Kenicutt et al. 1985, Sibuet et al. 1988). Jensen (1986) analysed the structure of the nematode communities from brine seeps in the Gulf of Mexico, and compared them with those in adjacent oxic sediments. Shirayama & Ohta (1990) identified the nematodes from a bathyal cold seep off Hatsushima, central Japan, and again compared them to those at an oxic reference station. The brine seep sediments in the northwest Gulf of Mexico are dominated (up to more than 90%) by 1 species belonging to the genus *Desmolaimoides*. Towards the edge of the seeps *Marylinnia* or *Rhyps* are dominant but at lower relative abundances (30 to 40%). A completely different community was present in the adjacent oxic sediments, where these 'sulphidic' species were lacking. The associations of oxybiotic species are much more diverse in terms of number of species than those in the sulphidic communities. The latter are characterized by increasing dominance with increasing sulphide concentrations. The center of the seeps seems to support only a few species (Jensen 1986). At the Hatsushima cold seep (Shirayama & Ohta 1990) the single-species dominance was less pronounced. The dominant genus *Daptonema* was represented by 2 species, each occurring in equal proportions of about 18%. At the well-oxygenated control area in that study the relative abundance of the dominant species, which belonged to the genus *Microlaimus*, was even higher (25%) than at the seep site.



More widespread than the cold seeps are the sulphide-rich, black sediment layers of eutrophic marine bottoms that are present from tidal flats to the deep sea. Only 2 studies of organically enriched, oxygen-poor sediments allowed a quantitative comparison with the nematode communities of hydrothermal vents. One is a study along an intertidal flat of the island of Sylt (German Bight, North Sea) by Wetzel et al. (1995). Both oxic and anoxic sediments were collected for analysis of the nematode species composition. The second study investigated the temporal changes in nematode species composition of a muddy, sheltered bay, Kilviken, on the Swedish coast. At this sampling site, sediments were seasonally covered by hypoxic bottom water (Hendelberg & Jensen 1993). Anoxic sediments at the Isle of Sylt (Wetzel et al. 1995) were dominated by 1 *Calo-microlaimus* species (64%). In the oxic control site sediments the dominance was shared between a *Metachromadora* species, a *Viscosia* species and a *Daptonema* species, each representing 15 to 26% of the nematode community. The hypoxic sediments at Kilviken (Hendelberg & Jensen 1993) were dominated (72%) by *Sabatieria pulchra*, a species known to have its population maximum in the Redox Potential Discontinuity (RPD) layer. The second most abundant genus was *Molgolaimus* representing 10% of the total community.

### Similarity analysis

CA based on the relative generic composition of all reduced environments—from hydrothermal vents (Iheya: Shirayama 1992, this study) and cold seeps (Gulf of Mexico: Jensen 1986; Hatsushima: Shirayama & Ohta 1992) to eutrophic sediments (Kilviken: Hendelberg & Jensen 1993; North Sea: Wetzel et al. 1995), and their oxic reference samples—demonstrates that the highest affinity is between all bathyal samples independent of their geochemical origin. In this ordination, data from the review of Soetaert & Heip (1995) of different bathyal sites in the NE Atlantic and the Mediterranean are included in order to compare the NE Pacific reference stations with other sites from the deep sea. The shallow reduced environments each have the closest relationship with their controls, if present. However, most of the Gulf of Mexico stations, both oxic (O Gmex) and thiobiotic (T Gmex), still show some separation when classified along the first 2 ordination axes. Therefore, in the final ordination 4 stations, 2 oxic and 2 thiobiotic (each time the most centrally positioned in the first analysis, which is not shown) were selected in order to perform the final CA shown in Fig. 5. The hydrothermal communities from the Fiji Basin (GTVs) show the highest affinity with their control MC samples. These deep-sea sediments do not deviate much

from bathyal nematode communities at similar depths (rise and slope) in the North Atlantic and adjacent seas, as reviewed by Soetaert & Heip (1995). Also, the hydrothermal sample from the Iheya ridge together with the bathyal cold seep from Hatsushima cluster with the other deep-sea samples. A second CA (Fig. 6), how-

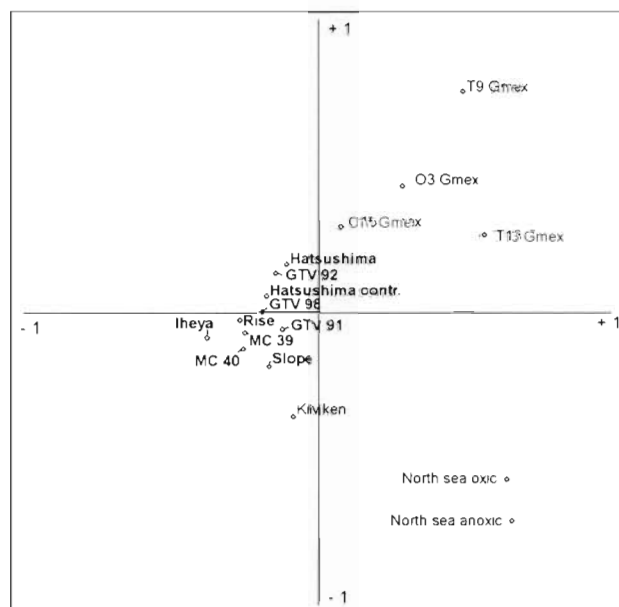


Fig. 5. First 2 ordination axes of a CA based upon the genus composition of all reduced stations and their controls (bathyal stations are indicated in bold). Eigenvalues: axis 1, 0.5851; axis 2, 0.4716; axis 3, 0.4549

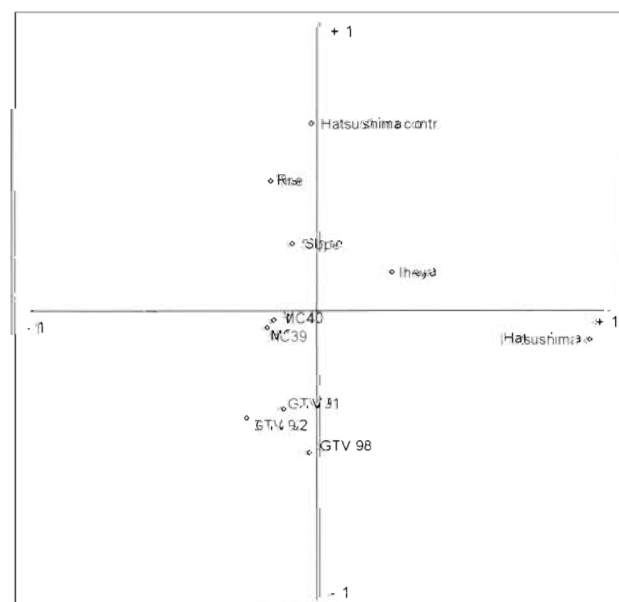


Fig. 6. First 2 ordination axes of a CA based upon the genus composition of all bathyal stations and their controls. Eigenvalues: axis 1, 0.6361; axis 2, 0.5577; axis 3, 0.5142

ever, in which all shallow stations are excluded, confirms the affinity of the hydrothermal Fiji samples (GTV) with their controls (MC).

Thus, there is neither a special affinity between hydrothermal nematode communities, nor between hydrothermal communities and genus associations from other reduced environments such as seeps or subsurface anoxic sediments in organically enriched areas. Multivariate analysis illustrates that each of the reduced spots has the highest affinity with its adjacent reference samples.

Only some abundant genera, each represented by one dominant species in the Fijian hydrothermal sediments, are frequently found in other reduced environments. For instance *Oncholaimus campylocercoides* is the only species at the center of shallow seeps off Milos (Crete; Thiermann et al. 1994). Towards the edges of the seeps, the number of species increases, with *Molgolaimus* being one of the few other genera represented (Thiermann unpubl.). *Molgolaimus* is often common in reduced conditions, such as the hypoxic bottom at Kilviken (Hendelberg & Jensen 1993). At the same location, the genus *Sabatieria* was represented in the thiobiotic community by 1 species, *S. pulchra*. Also, other *Sabatieria* species such as *S. punctata* and *S. longispinosa* are often the only remaining species in the most stressed situations, such as under high pollution pressure or towards the centre of cold seeps (Jensen 1986, Dando et al. 1993, Thiermann et al. 1994). In addition, this genus is frequently recorded in bathyal communities at depths of 2000 m (Soetaert & Heip 1995). However, *Sabatieria* is not present in any of the sediment samples from the Fiji Basin. Some *Leptolaimus* species are known to be very abundant at eutrophic estuarine stations (Soetaert et al. 1995). This genus is also often found at subdominant abundances in the deep sea (Vincx et al. 1994, Soetaert & Heip 1995).

### Size spectra

Thiobiotic species are often characterized by a high length-width ratio. Jensen (1986, 1987) suggested that this increased the surface area, allowing a higher cuticular uptake of dissolved organic matter and oxygen. The geometric mean body sizes indicate that the nematodes in the hydrothermal samples of the North Fiji Basin are relatively large. The mean length-width ratio is indeed higher than in the control samples of this area. However, this ratio is not as high as observed in some thiobiotic settings: relatively small species such as *Leptolaimus* sp., *Molgolaimus* sp. and *Monhystera* sp. dominate the communities, in contrast to the larger species of the genera *Oncholaimus*, *Pontonema*,

*Sabatieria* and the group of the Stilbonematinae which are characteristic for seeps, organically enriched bottoms and the black sediments beneath the RPD layer (see review in Giere 1993). Comparison of the size spectra from the hydrothermal communities, their controls and the nematode associations from inactive hydrothermal sites illustrates the shift of the spectra over 2 geometric size classes, while the morphological diversity remains similar.

### Biodiversity

The most striking trend along the gradient towards the center of hydrothermal activity is the decrease in species diversity and the increase in abundance of a few species. At the genus level, or even on a functional-morphological basis, the reduction of diversity from control areas towards hydrothermal sediments is much less pronounced. The extremely high nematode species diversity of the Fijian non-vent sediments is not exceptional compared to other deep-sea areas (Soetaert et al. 1991, Gage 1996).

Stress of many kinds, from chemical and physical to biological, often results in a significant decrease in biodiversity. On longer time scales, the extreme conditions in terms of chemistry and temperature conditions at hydrothermal sites have led to the presence of well-adapted, endemic macro- and megafauna that have much higher biomass than normal deep-sea communities (Desbruyeres et al. 1994). Although the overall diversity of the macro- and megafauna often decreases from unaffected deep-sea sediments towards hydrothermal sites, the local diversity at specific sulphide-rich sites can be quite high in comparison with oxic deep-sea sediments. This is especially the case for oligotrophic deep-sea areas where low densities lead to a low number of species. Due to aggregation at hydrothermal sites, a high number of hydrothermal macrospecies live within a small surface area (Desbruyeres et al. 1994). However, hydrothermal macrofauna communities that are geographically distributed all over the world harbour identical species. For example, only 1 species of vestimentiferan worm is recorded for the whole NE Pacific (Tunnicliffe & Fowler 1996).

### Origin of hydrothermal nematode communities: dispersal and colonization

A recent review by Tunnicliffe & Fowler (1996) on similarities between global hydrothermal vent fauna (excluding the nematodes and ciliates) concludes that plate tectonic reconstructions are in agreement with the present faunal relationships. Thus ridge pathways

seem to be the key to distribution patterns of the larger fauna. Larval stepping stones such as hotspots and whale carcasses (Bennett et al. 1994) are proposed as an additional mechanism for the distribution of certain groups. Among the nematodes, specialized forms exclusively associated with sulphidic conditions are also widely distributed in shallow marine environments. They often live in symbiosis with microorganisms; for example, *Astomonema*, a mouthless nematode, has extracellular bacteria filling the lumen of a modified gut (Ott et al. 1982, Giere et al. 1995), and species of the Stilbonematinae are covered by a fur of epibacteria. Only for the last group, however, is there good evidence for chemoautotrophic activity (Ott & Novak 1989, Ott et al. 1991). Stilbonematinae are most abundant in sulphidic sediments of tropical beaches from Bermuda and Belize (Ott & Novak 1989, Schiemer et al. 1990, Ott et al. 1991, 1995). They are frequently found in the deeper anoxic layers of sandy sediments off Florida (Ott et al. 1982), the Adriatic Sea (Ott et al. 1995), the North Sea (Warwick 1971, Lambshead 1986, Vanreusel 1991) and the Baltic Sea (Jensen 1987). Stilbonematinae have also been recorded at shallow seeps off Crete (Thiermann et al. 1994) and New Zealand (Kamenev et al. 1993). The mouthless nematode genus *Astomonema* was first observed in sulphidic sediments at the coast off California (Ott et al. 1982). Further records of *Astomonema* are from the North Sea (Dando et al. 1991, Austen et al. 1993) and the Adriatic Sea (Vidakovic & Boucher 1987). Shallow subsurface anoxic sediment layers and cold seeps are relatively persistent in time. In addition, sediment anoxia due to eutrophication is frequently found in shallow waters. Therefore, these environments provide a more or less continuous dispersal route for specialized life forms among the nematodes.

The limited number of observations on small sediment-dwelling organisms from hydrothermal environments suggests different colonization strategies for these isolated deep-sea habitats. These observations, which are in sharp contrast with data for the macro- and megafaunal species associations of reduced environments, can be summarized as follows. There is no taxonomically specialized or endemic nematode community present at the genus level. There is a relatively high similarity between the hydrothermal nematode communities and the adjacent deep-sea sediments in terms of genus composition, but none of the species is common to both oxic and sulphidic habitats. Although the biodiversity on a generic or functional-morphological level does not deviate greatly from the control areas, the species diversity is much lower in hydrothermal sediments. Proceeding from the control sediments to the hydrothermal vents, there is a shift in size spectra towards larger nematodes. This might be an

advantage in thiobiotic conditions, as was suggested by Jensen (1987). Finally, there is no strong affinity at the generic level with other reduced environments such as seeps or organically enriched sediments.

Nematodes have no planktonic life stage and their small size makes it difficult for nematode species to migrate between isolated hydrothermal patches as suggested by Tunnicliffe & Fowler (1996) for larger hydrothermal animals. The dispersion of nematodes is much more dependent on the spatial continuity of the habitat on a relatively small scale on the one hand, and on their tolerance for various environmental conditions on the other. In view of the instability of hydrothermal systems over small time periods, it is concluded that for deep-sea nematodes living in hydrothermal sediments, invasion from adjacent sediments that are potentially influenced by a different geochemical regime is much more important than the distribution of a strongly specialized fauna over long distances. The similar generic—but diverging species—composition between hydrothermal vents and adjacent deep sea sediments possibly indicates that among oxic colonizers, certain taxa that are less competitive in the usual oxic living conditions of the deep sea are able to colonize the nearby sulphidic islands successfully. Intensive sampling in combination with taxonomic DNA analysis may reveal new insights regarding these evolutionary aspects of hydrothermal nematodes.

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