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Patterns of nematode diversity at hydrothermal vents on the East Pacific Rise

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Abstract: The diversity and abundance of meiofauna in quasi-quantitative samples collected from *Bathymodiolus* mussel beds in a deep-sea hydrothermal vent field on the East Pacific Rise (EPR) was studied with particular reference to nematodes. Copepods, polychaetes and nematodes were found to be the most abundant meiofaunal taxa at all sites processed so far. Species richness (S = 4- 6), Shannon-Wiener diversity indices ($H'_{\log e}$ = 0.9-1.5) and Pielou's eveness indices (J' = 0.5-0.8) were similar at all sites. Six different species of nematode were identified, both sites exhibiting a dominance of Monhystrid species. Cluster analysis of Bray-Curtis similarities using group-average linkage on standardised data shows that samples from Train Station and East Wall separate out at around the 45% similarity level. This separation results from the different abundances of nematode species present at both sites and the exclusive presence of *Thalassomonhystera* sp. B at Train Station and *Anticoma* sp. A at East Wall. A pot sample from a mussel bed at "Oasis" at 17 25' S on the EPR exhibits approximately 30% similarity with the NEPR samples as a result of higher abundance and species richness of nematodes. To date, meiofauna have seldom been included in ecological studies at vents and it is therefore not clear to whether patterns of faunal zonation and biogeography similar to those known in megafauna are also present in this size class. Future work may reveal possible large-scale variation in nematode species richness.

Keywords: Nematodes • Meiofauna • Mussel beds • Hydrothermal vents

Introduction

Deep-sea hydrothermal vents are remarkable for their spectacular megafauna, many of which appear to have a high level of endemicity to these chemosynthetic environments. Meiofaunal studies of vents, however, have largely been confined to species present in qualitative macrofaunal samples and a limited amount of work has been done on the meiofauna of deep-sea reducing environments in general. At vents this is chiefly due to a lack of soft sediment precluding quantitative core sampling at most sites. *Bathymodiolus* mussel beds, however, are present at many deep-sea hydrothermal vents, providing ecological units for studying patterns of macro- and meiofaunal diversity and abundance in these habitats (Van Dover, 2003).

This study examines the diversity and abundance of meiofauna in quasi-quantitative samples collected from *Bathymodiolus* mussel beds in a deep-sea hydrothermal vent field on the East Pacific Rise (EPR) with particular reference to nematodes. To date, meiofauna have seldom been included in ecological studies at vents and it is therefore not clear to whether patterns of faunal zonation and biogeography similar to those known in megafauna are also present in this size class. In a wider context, the presence of positive latitudinal gradients in nematode species richness with organic flux in the deep-sea is a topic of debate and work at hydrothermal vents may eventually provide a natural "control" for such studies if the energy supplied to their inhabitants can be assumed not to vary with latitude. This paper identifies major meiofaunal taxa and dominant nematodes at hydrothermal vent mussel beds on the EPR, examines small-scale variation in the composition of the meiofaunal community and reveals large-scale patterns in nematode distribution along the EPR.

Materials and Methods

Study sites, sample collection and processing

Details and maps of the vent field and sites used in the current study are given in Van Dover (2003). The two sites sampled were situated at 9°50' N on the northern East Pacific Rise (NEPR). Samples of mussels and their associated invertebrates were collected by the submersible Alvin during November 1999 using a quasi-quantitative "pot" sampler. This device, described in Van Dover (2003), samples a variable mussel volume from a mussel bed area of 531 cm^2; the volume sampled is subsequently determined aboard ship. At the sites sampled for this study (Train Station and East Wall), mussels occupied low-temperature (< 10°C) flow zones associated with cracks in lobate basalt lavas and were adjacent to clusters of vestimentiferan tubeworms *Riftia pachyptila*. Six quantitative samples were made at each of these two separate sites. At Train Station, pot samples were collected along a 5 m transect from the periphery of the field to a central clump of tubeworms *Riftia pachyptila*. The location of samples collected from the East Wall site was haphazard.

Samples were washed through a 63 µm aperture sieve, preserved in buffered 10% formalin and stored in 70% EtOH. They were subsequently sorted into major taxa (this included both the permanent and temporary meiofauna) to quantify their abundance and the nematodes mounted on slides in anhydrous glycerine. These mounts were then examined under high power and drawings made of major morphological features to aid taxonomic identification to species level wherever possible.

Abundance and diversity analyses

Number of individuals per litre of mussel volume was calculated from the raw abundance data for all meiofaunal taxa and for all nematode species identified. In order to compare these mussel pot samples to other meiofauna studies, abundance values were also standardized to 10 cm^2. EstimateS (Colwell, 1997; randomization operations = 100, without replacement) was used to randomize the sample data and eliminate the effect of sample order. For analysis of species richness, sampling effort was expressed as the cumulative number of individuals sampled. Primer v5 (Clark & Gorley, 2001) was used to carry out a hierarchical agglomerative cluster analysis of Bray-Curtis similarities on standardised nematode species composition data of all pot samples (using group-average linkage).

Results

Major Taxa

Copepods, polychaetes and nematodes are the most abundant meiofaunal taxa at all sites processed so far (Fig. 1). Other taxa present at much lower abundance included foraminiferans, ostracods, gastropod larvae and mites (Table 1). At Train Station, copepods were found to be the most abundant taxon in all pot samples (Fig. 1A). This trend is also apparent at East Wall in 5 out of the 6 samples (Fig. 1B). Abundances of all meiofaunal taxa were low at Train Station in comparison to East Wall. This was particularly notable in nematodes, with values ranging from 5 to 167 per litre of mussel volume (< 1-5 individuals per 10 cm^2) at Train Station compared to 1 to 1387 per litre (< 1-51 individuals per 10 cm^2) at East Wall. The transect of pot samples across the mussel bed at Train Station allows some assessment of small-scale spatial variability and possible zonation in the composition of meiofauna, although cautious interpretation of these data is required in the absence of replication. Nematodes, however, were rare in the sample from the outer edge of the mussel bed, reach their highest abundance in the centre of the mussel beds, then decline towards the inner edge (Fig. 1A). This trend is less apparent in the copepods and polychaetes, although these taxa were most abundant in pots 2, 3 and 4 in the centre of the transect.

Small-scale spatial variation in nematode species richness

For a given sampling effort, where effort is expressed in cumulative number of individuals sampled (Fig. 2) species richness from the two sites at 9°N combined was apparently low compared to normal deep sea (Vanreusel et al., 1997). Species richness (S = 4-6), Shannon-Wiener diversity indices (H'log e = 0.9-1.5) and Pielou's eveness indices (J' = 0.5-0.8) were similar at all sites. Six different species of nematode were identified, both sites exhibiting a dominance of Monhystrid species. At Train Station, the most abundant Monhysterid species was *Geomonhystera* sp. A followed by *Thalassomonhystera* sp. A, whereas at East Wall the dominance of these two species was reversed

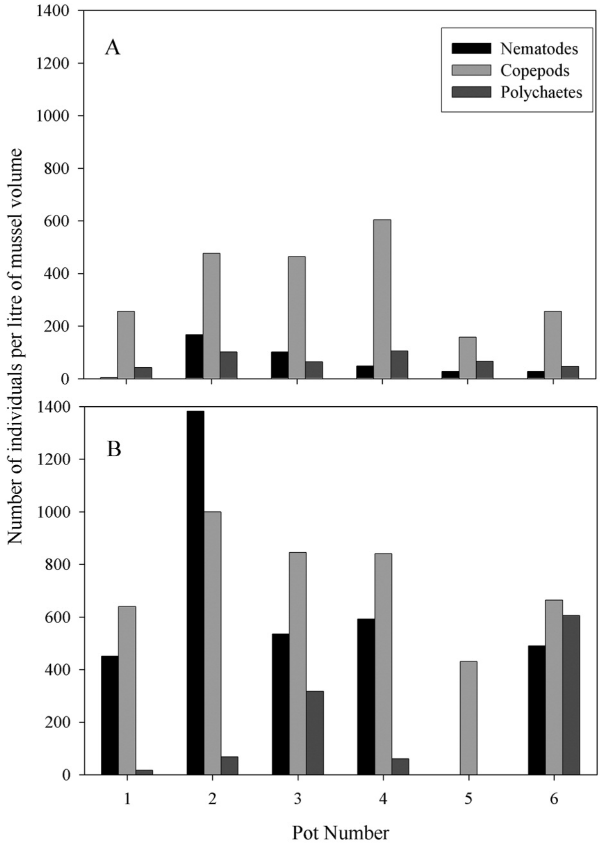

Figure 1. Abundance of major meiofaunal taxa in quasi-quantitative pot samples from 9°N on the East Pacific Rise. **A.** Across a transect at Train Station (pots 1-6 moving deeper into the mussel bed). **B.** Taken haphazardly from the East Wall mussel bed.

Figure 1. Abondance des principaux taxons de méiofaune des prélèvements quasi quantitatifs de la Ride Pacifique Orientale (9°N). **A.** Sur le transect à Train Station (pots 1-6 vers la partie profonde de la moulière). **B.** Pris au hasard dans la moulière de East Wall.

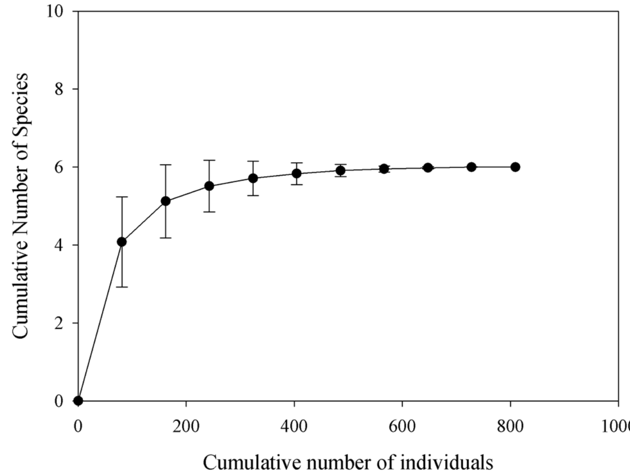

Figure 2. Species accumulation curve for nematode species in meiofaunal samples from Train Station and East Wall at 9°N on the East Pacific Rise: effort based on cumulative number of individuals. Data points are means (± 95% CI, randomizations = 100, without replacement).

Figure 2. Courbe cumulée du nombre d'espèces de nématodes des échantillons de méiofaune de Train Station et de East Wall (Ride Pacifique Orientale, 9°N) en fonction du nombre cumulé d'individus. Moyennes (± intervalle de confiance à 95%, tirages aléatoires = 100, sans remise).

(Fig. 3). *Thalassomonhystera* sp. B was only present at Train Station and *Anticoma* sp. A exclusive to East Wall. A single species of Linhomoeid (Linhomoeidae sp. A) and a single species of Chromadorid (Chromadoridae sp. A) were also present in low abundance at both sites compared to the Monhysterids.

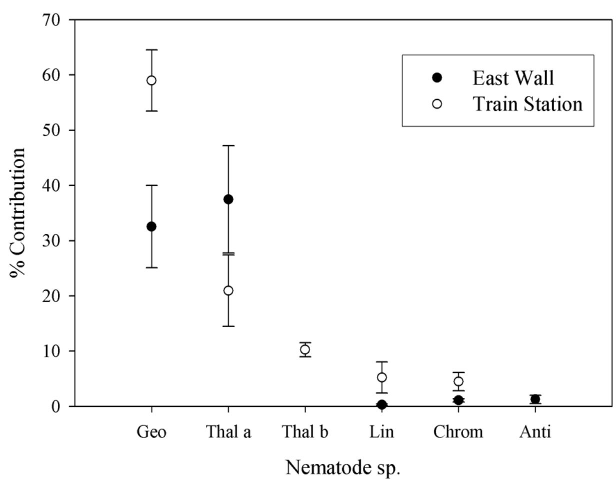

Figure 3. Rank order of nematode species abundances in meiofaunal samples from Train Station and East Wall at 9°N on the East Pacific Rise. Data shown are mean contributions of each species to the total abundance of nematodes per litre of mussel volume. Error bars depict 95% confident interval for each mean, n = 5 in each case. Geo: *Geomonhystera* sp. A; Thal a: *Thalassomonhystera* sp. A; Thal b: *Thalassomonhystera* sp. B; Lin: Linhomoeidae sp. A; Chrom: Chromadoridae sp. A; Anti: *Anticoma* sp. A.

Figure 3. Dominance relative (%) des principales espèces de nématodes de la méiofaune de Train Station et de East Wall (Ride Pacifique Orientale, 9°N), calculée sur l'abondance totale de nématodes par litre de volume de moules. Les barres représentent l'intervalle de confiance à 95%, n = 5 pour chaque moyenne. Geo: *Geomonhystera* sp. A; Thal a: *Thalassomonhystera* sp. A; Thal b: *Thalassomonhystera* sp. B; Lin: Linhomoeidae sp. A; Chrom: Chromadoridae sp. A; Anti: *Anticoma* sp. A.

Table 1. Data set of number of individuals of higher taxa per 10 cm^2 of mussel pot surface area. (Train Station: TS1 – TS6; East Wall: EW1 – EW6; Oasis: O3).

Tableau 1. Nombre d'individus des taxons supérieurs par 10 cm^2 de surface des pots de moules prélevés. (Train Station: TS1 – TS6 ; East Wall: EW1 – EW6 ; Oasis: O3).

	TS1	TS2	TS3	TS4	TS5	TS6	EW1	EW2	EW3	EW4	EW5	EW6	O3
Mussel Volume	3.8	1.5	1.5	1.9	3.8	3.9	1.4	1.4	1.6	4.6	3.0	2.5	3.5
Nematodes	0.3	4.7	2.9	1.7	2.0	2.1	11.9	36.5	16.1	51.3	0.1	9.2	45.9
Copepods	18.3	13.5	13.1	21.6	11.3	18.8	16.9	26.4	25.5	72.8	24.3	12.5	22.2
Polychaetes	3.0	2.9	1.8	3.8	4.8	3.5	0.5	1.8	9.6	5.3		11.4	3.0
Mites	0.1	0.1				0.1							
Ostracods													0.2
Foraminiferans													0.5
Gastropod larvae								0.2		0.2			0.9

Large-scale variation in nematode species richness

Cluster analysis of Bray-Curtis similarities using group-average linkage on standardised data (Fig. 4) shows that samples from Train Station and East Wall separate out at around the 45% similarity level. This separation results from the different abundances of nematode species present at both sites and the exclusive presence of *Thalassomonhystera* sp. B at Train Station and *Anticoma* sp. A at East Wall. Train Station Pot 1 is a clear outlier as a result of its very low abundance value of of 5 nematodes per litre of mussel volume (< 1 individual per 10 cm^2). A pot sample from a mussel bed at "Oasis" at 17°25' S on the EPR was included in this analysis and to give an indication of how future work may reveal possible large-scale variation in nematode species richness. This sample exhibits approximately 30% similarity with the NEPR samples as a result of higher abundance and species richness of nematodes. Table 2 shows the percentage composition of nematode species from the 13 mussel pot samples (including Oasis).

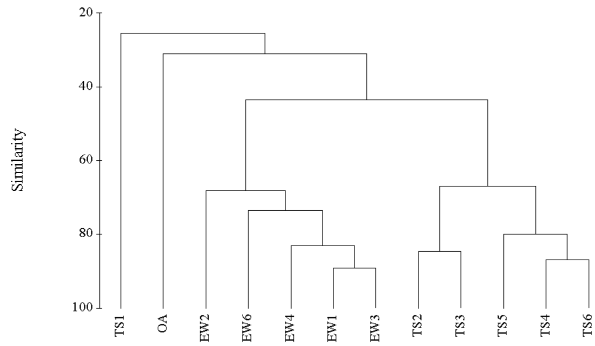

Figure 4. Cluster analysis of Bray-Curtis similarity for nematodes in meiofaunal samples from the East Pacific Rise using group-average linkage on standardised data. **EW.** East Wall. **TS.** Train Station. **OA.** Oasis. 1-6: sample number.

Figure 4. Dendrogramme (lien par groupement moyen) réalisé à partir de l'indice de similarité de Bray-Curtis (données standardisées) calculé sur les abondances de nématodes des échantilllons de méiofaune de la Ride Pacifique Orientale. **EW.** East Wall. **TS.** Train Station. **OA.** Oasis, SEPR. 1-6: numéro de l'échantillon.

Discussion

Compared to studies of megafauna, there has been a limited amount of work on the meiofauna of deep-sea vents and seeps. The first observations of meiofauna from hydrothermal vents on the EPR were described by Dinet et al. (1988), who reported meiofaunal densities of one or two orders of magnitude lower than the non-vent deep-sea. Since then, further studies have indicated an increase in number of meiobenthic animals, a reduction in diversity and increased predominance of nematodes at vents and seeps compared to normal deep sea sediments (Jensen, 1986; Fricke et al., 1989; Montagna et al., 1989; Shirayama & Ohta, 1990; Kamenev et al., 1993). It could be suggested by the presence of only three dominant meiofaunal taxa at both sites in the current study that some meiofauna taxa find it difficult to adapt to the vent environment. Giere et al. (1991), however, have suggested that anoxic and sulphidic chemoclines provide a good food source for meiofauna and a habitat with low competition and predation, but only if meiofaunal species are able to tolerate the toxic effects of sulphide.

Samples at Train Station were collected along a transect across the mussel bed, enabling a first examination of possible zonation in the meiofauna in this environment. The abundances of nematodes, copepods and polychaetes varied between samples along this transect (Fig. 1A). From pot 2 inwards, nematodes declined in abundance with distance into the mussel bed. A similar pattern is suggested in the polychaetes. Copepod abundances were variable in

Table 2. Percentage composition of nematode species from 13 mussel pot samples (Train Station: TS1 – TS6; East Wall: EW1 – EW6; Oasis: O3).
Tableau 2. Abondance relative (%) des espèces de nematodes de 13 prélèvements de moules (Train Station: TS1 – TS6; East Wall: EW1 – EW6; Oasis: O3).

	TS1	TS2	TS3	TS4	TS5	TS6	EW1	EW2	EW3	EW4	EW5	EW6	O3
Geomonhystera sp.A	38.5	67.0	64.4	42.4	43.6	63.4	48.0	43.0	3	52.6		43.3	4.0
Thalassomonhystera sp.A	46.2	9.6	10.2	15.2	25.6	7.3	42.7	45.6	55.3	42.1		51.3	10.8
Chromadoridae sp.A		5.3	1.7	9.1	2.6	4.9	1.3	1.9	0.7	2.0		2.0	11.2
Juvenile Monhysteridae	7.7	3.2	11.9	21.2	5.1	9.8	4.0	8.2	12.7	2.6		1.3	1.2
Thalassomonhystera sp.A	7.7	12.8	8.5	9.1	5.1	12.2							24.8
Linhomoeidae sp.A		2.1	3.4	3.0	17.9	2.4		0.6		0.7		2.0	
Anticoma sp.A							4.0	0.6	1.3				6.4
Draconematidae sp.A													15.2
Chromadoridae sp.B													2.8
Cythalaimidae sp.A													8.4
Leptolaimidae sp.A													8.8
Microlaimidae sp.A													4.8
Polysigma sp.A													0.4
Desmodoridae sp.A													1.2

pots 1 to 4 but appeared lower in pots 5 and 6. A difference in temperature was noted between the mussels on the edge of the bed where the first pot was taken and the edge of the tubeworm clump where the transect ended (CL Van Dover, pers. comm.). Giere (1993) has suggested that temperature may have a major influence on meiofaunal community structure and this may be a factor here. Energy availability is another factor which could potentially influence community structure across the transect at Train Station. A recent study of nematode abundance at a whale fall site (Debenham et al*.,* 2004) reported nematode abundance to be positively correlated with distance from the carcass, suggesting that organic input may also be a factor in the small-scale variation found here. Hydrothermal flux can vary at small scales in the vent habitat, which may create a gradient in productivity (Mullineaux et al., 2003). The abundance of meiofauna in the samples from Train Station is low, however, compared to those from East Wall and other studies. It may be that meiofaunal abundance is related to the quantity of sediment in the sample and this may vary per unit mussel volume between sites. Abundance values may also be confounded by the occurrence of vertical gradients in meiofaunal distribution. These may have been disrupted and masked by the nature of the material sampled and the sampling device used. Information on sediment properties would also be desirable here. Quantification of these factors in the pot samples requires further investigation.

One nematode species from the genus *Geomonhystera*, two from *Thalassomonhystera,* one genera and species from Linhomoeidae and Chromadoridae respectively were identified in the samples from Train Station. One additional species from the family Anticomidae, genus *Anticoma* was also found at East Wall. The species/genus ratio found in all samples at both these sites is therefore very low, with high dominance of Monhysterids. These features were apparent in all samples regardless of mussel bed location (Fig 3). Vanreusel et al. (1997) reported an equally low species/genus ratio of 1 for 27 genera found in other hydrothermal mussel bed samples. The numerically dominant genera in their study were *Leptolaimus* and *Monhystera* both of which had 2 species. The nematode genera found in the current study were also found in samples from tubeworm washings at hydrothermal vents analysed by Dinet et al. (1988) and in sediment core at a cold seep (Shirayama & Ohta, 1990).

The cold seep nematodes studied by Shirayama & Ohta (1990) showed a strong affinity with the assemblage of an adjacent, non-chemosynthetic location rather than the meiofauna of another chemosynthetic site nearby. One limitation of the current study is that no samples were taken of reference sediments of non-hydrothermal sediment in close proximity to the vent site. This prevents comparison of species richness or types of species present between vent environments and adjacent sediments. The reference samples in the Vanreusel et al. (1997) study which were characterized by a very high species/genus ratio. Out of the 2 reference samples, individuals of 42 other genera were found. It was noted that although several genera were common for both hydrothermal and reference sediments, none of the species present in the reference sediments were found in the hydrothermal sediments. This finding emphasizes the need to work to species level in these habitats.

The majority of the nematode species identified here were present at both the vent sites studied. The separation of samples between the sites in cluster analysis (Fig. 4) therefore results largely from differences in the relative abundance of these species (Fig. 2). The sample from the southern East Pacific Rise ("Oasis") included in the cluster analysis, however, has greater diversity in its species composition with species from 5 additional families: Draconematidae, Cythalaimidae, Leptolaimidae, Microlaimidae, and Desmodoridae. The species from *Thalassomonhystera*, *Geomonhystera* and Chromadoridae found at 9°N were present at Oasis but were not the numerical dominants at this site. This finding suggests possible biogeographic patterns in meiofauna that will be examined in future work; Four sites on the SEPR including Oasis are currently being worked on as well as samples from an additional mussel bed transect at 9°N. Results from these additional samples will confirm the small-scale patterns found. To date, meiofauna have seldom been included in ecological studies at vents and it is therefore not clear to whether patterns of faunal zonation and biogeography similar to those known in megafauna are also present in this size class.

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