

Hydrothermal vent meiobenthos associated with mytilid mussel aggregations from the Mid-Atlantic Ridge and the East Pacific Rise

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Abstract

Deep-sea hydrothermal vents occur along the mid-ocean ridges and back-arc basins around the globe. There are very few community analyses of vent meiobenthos. The central objectives of this study were to identify and quantify for the first time the entire metazoan meiobenthic community associated with mussel aggregations of *Bathymodiolus thermophilus* Kenk and Wilson, 1985 from the EPR, 11°N and of *Bathymodiolus puteoserpentis* Cosel et al., 1994 from the Mid-Atlantic Ridge (MAR), 23°N. Using a quantitative sampling method, abundance, biomass, sex ratio, species richness, diversity, evenness, and trophic structure were studied based on three samples from each site. Meiobenthic abundance in each sample was unexpectedly low, but similar between sites. The community was composed of nematodes, copepods, ostracods, and mites, with a total of 24 species at EPR vents, and 15 species at MAR vents. While most copepod species were vent endemics within the family Dirivultidae, nematodes and harpacticoid copepods belonged to generalist genera, which occur at a variety of habitats and are not restricted to hydrothermal vents or the deep sea. The meiobenthos of hydrothermal-vent mussel beds constitutes a unique community unlike those of other sulfidic habitats, including the thionios of shallow-water sediments and the meiobenthos of deep-sea, cold-seep sediments. The trophic structure was dominated by primary consumers, mainly deposit feeders, followed by parasites. Predatory meiofaunal species were absent.

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1. Introduction

Mid-ocean ridges are sea-floor spreading centers with volcanic, tectonic, and hydrothermal activity. Extending more than 75,000 km around the globe,

they are an almost continuous volcanic mountain chain situated at bathyal and abyssal depths (1500–4000 m) with hydrothermal vents scattered along their length (see Van Dover, 2000). At hydrothermal vents, biological communities are present within areas where reduced (sulfide, methane) and oxidized (oxygen, nitrate) compounds are readily available because of the thermal and the chemical gradients resulting from mixing of

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hydrothermal fluid with cold seawater. The inherently unstable physico-chemical conditions with abrupt temperature and pH gradients, and the toxicity of vent emissions, dictate that organisms living at vents must be adapted to these extreme conditions (e.g. Childress and Fisher, 1992). Striking spatial patterns of typical macrofauna assemblages along a gradient of hydrothermal fluid flux can be distinguished (e.g. Hessler and Smithey, 1983; Hessler et al., 1985; Shank et al., 1998). Hydrothermal vent habitats contrast sharply with abyssal, soft-sediment, non-vent areas with relatively stable physico-chemical conditions (Gage and Tyler, 1996).

Meiobenthos, animals and protists passing through a sieve with 1 mm mesh size and retained on a 63 μm (or smaller) mesh sized sieve (Giere, 1993), forms part of the hydrothermal vent community. This faunal component is poorly understood, as shown by the fact that the entire meiobenthic community has never been described from a single hydrothermal vent (Dinet et al., 1988; Shirayama, 1992; Van Harten 1992; Vanreusel et al., 1997). A few nematode species, usually the dominant taxon in meiofaunal communities, are described from sediments at the East Pacific Rise, the Guaymas Basin, the Lau Basin, and the North Fiji Basin (Decraemer and Goubault, 1997; Verschelde et al., 1998). However, not a single nematode associated with hard substrata, which dominate the hydrothermal vent ecosystem at the East Pacific Rise, has been described yet. This also holds true for many other taxa. The only exception is the Copepoda with 78 currently described species, and to a lesser extent, Ostracoda and Halacaridae (Gebruk et al., 1997; Tunnicliffe et al., 1998; Heptner and Ivanenko, 2002; see Bright, 2006). Comprehensive studies are necessary not only to understand the community structure of meiobenthos but also to provide an insight into the biodiversity of the entire animal community and their trophic interactions.

In this study, we chose two mytilid mussel beds from geographically distant hydrothermal vent areas but with similar hard-substrate, diffusive flow: *Bathymodiolus thermophilus* Kenk and Wilson, 1985 from the East Pacific Rise (EPR), Buckfield 11°N and *Bathymodiolus puteoserpentis* Cosel et al., 1994 from the Mid-Atlantic Ridge (MAR), Snake Pit 23°N. While the dominant macrofaunal invertebrates and the basic communities found along vent flux gradients differ between EPR and MAR

(Hessler and Smithey, 1983; Hessler et al., 1985; Rona et al., 1986; Van Dover, 1995; Gebruk et al., 1997; Desbruyères et al., 2001), mytilid mussel beds are known from all oceans (Fisher, 1990; Van Dover et al., 2002). At hydrothermal vents, they generally occur at moderate diffuse flow regimes with temperatures up to 10 °C (Hessler et al., 1985; Sarradin et al., 1999; Desbruyères and Segonzac, 1997; Desbruyères et al., 2001). The mussels form dense aggregations with their byssus threads creating a habitat with interstitial space in which associated small macro- and meiobenthos live (Van Dover and Trask, 2000; Van Dover 2002, 2003; Turnipseed et al., 2004; Dreyer et al., 2005). It is generally assumed that primary net productivity of free-living microbes at vents (rarely measured with 275 mg C m⁻² day⁻¹ in Lein and Pimenov, 2002; and about 4% C_{org} of POM in Levesque et al., 2005) supports the high densities of macrobenthic grazers and deposit feeders at vents (see Tunnicliffe et al., 2003). In addition, primary production of chemoautotrophic bacteria living as endosymbionts in the gills of the mussels (thiotrophic, sulfur-oxidizing endosymbionts in *B. thermophilus* and additionally also methanotrophic bacteria in *B. puteoserpentis*; Fisher et al., 1987; Cavanaugh et al., 1992; Fisher et al., 1993; Nelson et al., 1995; Robinson et al., 1998) indirectly contributes to the deposition of organic matter as feces and pseudofeces, which provide substrate and food for colonization of macro- and meiofauna.

The geological and hydrothermal settings differ between the MAR and the EPR. The spreading rate is slow at MAR (10–50 mm per year) but it is fast at EPR (>90 mm per year; Fornari and Embley, 1995). Distances between active hydrothermal zones are smaller at the fast-spreading EPR than at the slow-spreading MAR (Van Dover, 1995; Desbruyères et al., 2001). Furthermore, catastrophic volcanisms and tectonic activity are less frequent at MAR than at EPR (e.g. Van Dover, 2002, 2003).

The central objective of this study was to identify and quantify for the first time the permanent metazoan meiobenthic community associated with two mytilid mussel beds from EPR and MAR so that the species diversity, abundance, biomass, and trophic structure of the communities are documented. The following questions will be addressed: (1) Does meiobenthos associated with vent mussels exhibit low species richness and diversity, but high abundance, as expected for an environment with extreme conditions and high primary productivity?

(2) How similar are these meiobenthic communities from the EPR and MAR vent fields, which represent geographically distant, but environmentally similar habitats? (3) What is the trophic structure of these meiobenthic communities? (4) How does meiobenthic community structure in deep-sea vent mussel beds compare to that of other benthic communities?

2. Material and methods

2.1. Collection sites

Two vent sites were chosen for this study: Moose site in the Snake Pit vent field (23°22.16N 44°56.07W), MAR, and Buckfield vent field (11°24.90N 103°47.20W), EPR. At both vent fields, mussel beds (*B. thermophilus* at EPR and *B. puteoserpentis* at MAR) grew on bare basalt. Only a little sediment composed of mostly flocculent organic material with a few basaltic grains and sulfide precipitates was found between mussels.

The Buckfield vent field (Fig. 1) is located between the Orozco and Clipperton transform faults in the axial valley of the EPR at 2480 m depth. The mussel bed (~20–30 m maximum dimension) was formed of bands of *B. thermophilus* presumably following cracks or fissures rather than being a large continuous bed of mussels. At the time of collection, shimmering water emanated from the warmest parts of the mussel bed with temperatures approximately between 2 and 10 °C (Van Dover,

pers. obs.). Based on submersible observations of Buckfield in 1988, the mussel beds were at least 17 years old at the time of sampling.

The Snake Pit vent field (Fig. 1) lies south of the Kane transform fault, in the middle of the MAR axial valley (Karson and Brown, 1988). Based on submersible observations at Snake Pit in 1986 and subsequent years, small mussel beds have been present at Moose for more than 19 years. *B. puteoserpentis* were sampled from two adjacent linear (~3 m long, 1 m wide) bands of mussels over hairline fissures from which emanated warm, diffuse vent water (~5 °C) at 3492 m depth (Turnipseed et al., 2004).

2.2. Sample collections and processing

Using the submersible Alvin, 3 independent quantitative samples were collected with the ‘mussel pot’ sampling gear at the MAR and EPR vent sites during July and December 2001 (for details see Van Dover, 2002, 2003; Turnipseed et al., 2004). EPR and MAR always refer hereafter to the samples taken from the Buckfield and Moose (at Snake Pit) mussel beds, respectively. In all cases, samples were taken at least one mussel pot (i.e. ~50 cm) away from any others. The sampling pot (26 cm diameter, 26 cm height, 531 cm² surface area, 11.35 l volume), lined with a tightly woven kevlar bag, was pushed into the mussel aggregation until it reached the surface of the basalt and then closed. To prevent the loss of animals during transport, each pot was secured in a plastic quiver on the workbasket of the submersible.

On board the research vessel, mussel clumps were immediately disassembled and washed 3 times with 10 µm filtered seawater to wash off associated fauna and sediment. The efficiency of this extraction technique was confirmed by carefully searching for meiofauna on the remaining mussel shells in samples similar to the ones used for this study. The mussel volume per sample was determined by displacement of fresh mussels with shells immersed in seawater in a graduated container. The number of mussels per sample was counted and the volume of wet sediment (in our samples mostly particulate organic material) was measured (Table 1).

Washings from mussels were sieved onto a set of 250 µm and 63 µm sieves to retain the associated fauna. The retained organisms were preserved in 4% buffered formaldehyde for 24 h and stored in 70% ethanol. The ‘coarse’ fraction of samples

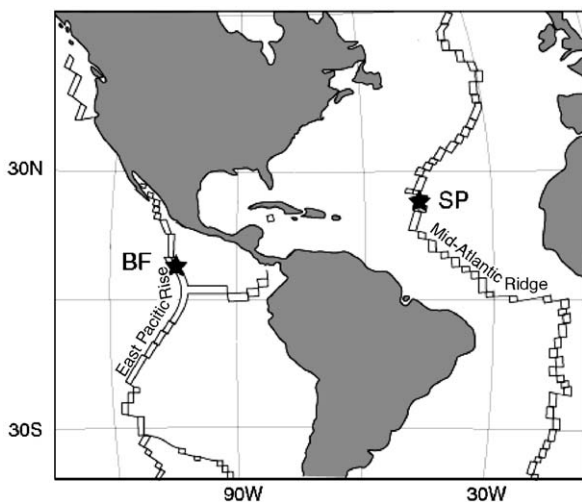


Fig. 1. Map of the two sampling sites, SP = Snake Pit vent field (23°22.16N, 44°56.07W), Mid-Atlantic Ridge, and BF = Buckfield vent field (11°24.90N, 103°47.20W), East Pacific Rise.

Table 1
Characteristics of study sites and samples

Sampling sites	Alvin dive No.	Mussels per sample	Mussel volume per sample (ml)	Sediment volume per sample (ml)	Mussel length (mm)
MAR1	3672	21	3900	12.5	79.1 ± 21.1
MAR2	3672	16	3500	14.3	88.9 ± 31.3
MAR3	3672	20	4000	12.5	79.9 ± 28.9
EPR1	3742	9	2800	7.5	163.6 ± 10.5
EPR2	3742	10	2550	7.4	146.3 ± 15.6
EPR3	3742	10	2700	9.7	154.2 ± 10.5

MAR = Mid-Atlantic Ridge, Snake Pit 23°22.160N, 44°56.07W; EPR = East Pacific Rise, Buckfield 11°24.90369N, 103°47.20360W; mussels collected per sample pot, mussel volume in ml and wet sediment volume in ml collected with each sample are given. Mussel length ± SD is the mean mussel length of mussels ± SD in mm collected per pot.

Table 2

Total counts of meiobenthos (total meiofauna excluding planktonic meiofauna and larvae/juveniles of macrobenthos) per pot sample, per 10 cm² surface area and per 1000 ml mussel volume, from each mussel collection

Samples	Meiobenthos per sample	Meiobenthos per 10 cm ² surface area	Meiobenthos per 1000 ml mussel volume
MAR1	2464	46	631
MAR2	1960	36	560
MAR3	2440	45	610
EPR1	1333	25	476
EPR2	1602	30	629
EPR3	1713	32	634

EPR1–EPR3 are pot samples 1–3 from East Pacific Rise and MAR1–MAR3 are samples 1–3 from Mid-Atlantic Ridge.

(> 250 μm) was stained with Rose Bengal and contained both macrofaunal and meiofaunal species. Macrofaunal data are reported elsewhere (Turnipseed et al., 2004; Dreyer et al., 2005). The “fine” fraction of samples (63–250 μm) was extracted from the remaining sediment by centrifugation with Ludox HS-40 (density = 1.3 g cm⁻³) 3 times as described by Burgess (2001) without staining. The efficiency of the extraction techniques was checked and no animals were encountered in the remaining sediment fraction. Total meiofauna from both size fractions of samples were picked out, sorted and counted. Only the permanent meiobenthos, i.e. benthic animals that are in the size range of meiofauna as adults, were included in this study, while planktonic species and juvenile macrofauna (mostly polychaetes and gastropods) were excluded (Table 2; Fig. 2).

All meiobenthic animals were counted and identified to higher taxa level. From each sample, 400 nematodes and copepod individuals were identified to species level, except for nematodes from EPR samples, where less than 400 individuals were found. The individuals were haphazardly

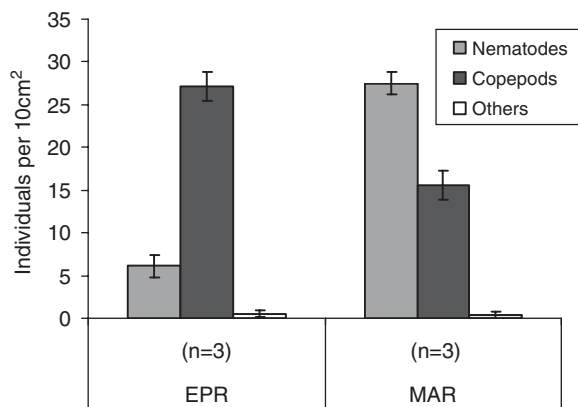


Fig. 2. Mean number of total meiobenthic individuals per 10 cm² from Mid-Atlantic Ridge (MAR) and East Pacific Rise (EPR) samples (mean ± standard deviation).

sorted out by carefully shaking the vial with the sample and the taking a drop of liquid (1–3 ml) with a syringe. All animals in this drop were identified. This process was repeated until the 400 individuals per phylum were reached. Mites and ostracods were very low in abundance (< 3 individuals per sample)

and were not included in biomass and sex-ratio calculations. The ostracod species at MAR and EPR were different species but were not identified further. Also, the mite species found at MAR was not identified further.

2.3. Quantification of abundance and biomass of meiobenthos

The abundance and biomass of meiobenthos from each sample was normalized from the surface area of each pot collected (531 cm²) to the commonly used standard surface area of 10 cm². The abundance of macrofauna associated with mussel aggregations usually has been calculated per 1000 ml mussel volume (measured as “mussel volume”; Van Dover and Trask, 2000; Van Dover, 2002, 2003; Turnipseed et al., 2004). To be able to draw comparisons between the two invertebrate size classes, macro—and meiobenthos, we also calculated the abundance of meiobenthos per 1000 ml mussel volume.

Individual biomass (μg wet weight) of nematode species was estimated according to Andrassy (1956) [$\text{wt} (\mu\text{g}) = \text{length} (\mu\text{m}) \times \text{width}^2 (\mu\text{m}) / 1600,000$; $\text{wt} = \mu\text{g}$ wet weight, $L = \text{length}$ (from anterior to posterior end) and $W = \text{maximum diameter of body}$]. All identified specimens were measured. The individual biomass (mg wet weight) of copepod species was estimated according to Chislenko’s nomograms (Chislenko, 1968). Nomograms consider wet weight of aquatic organisms according to body size and shape. Considering body form and the average size of a siphonostomatoid copepod with 1.04 mm length, the wet weight of one specimen was determined at about 0.090 mg (Chislenko, 1968; Heptner and Ivanenko, 2002). This seemed to be appropriate, as the family Dirivultidae belonging to the order Siphonostomatoida dominated the samples and its representatives, females and males, were all very similar in size and body shape. The biomass of harpacticoid copepods was estimated according to McIntyre and Warwick (1984) [$\text{wt} (\mu\text{m}) = l \times w^2 \times c$; $v = \text{volume}$, $l = \text{length}$, $w = \text{width}$, $c = \text{conversion factor}$ (= 400, corresponding to pyriform body form of measured harpacticoid copepods)]. Usually 30 females and 30 males per species were measured from the tip of the head to end of the furca, and from these data, a mean size for females and males of each species was estimated. When the number of males and females was less than 50, all specimens were measured. The

total biomass of nematodes and copepods was estimated by multiplying the mean biomass of each species by the total abundance of each species in each sample.

2.4. Feeding types

In free-living aquatic nematodes, the structure of the buccal cavity has proved to be a valuable indication of the feeding type. Wieser (1953) distinguished 3 types of primary consumers (selective deposit feeders with a small buccal cavity and non-selective deposit feeders with a large buccal cavity, both without teeth; grazers with a scraping tooth) and 1 type of secondary and tertiary consumers (omnivores, scavengers, and predators with teeth and/or large jaws). Copepods can also be divided into different feeding types according to their mouthparts and siphons. According to Heptner and Ivanenko (2002) three feeding types for benthic, hydrothermal vent copepods are suggested: type 1 (selective and unselective deposit feeders with a short and robust siphon) are primary consumers, type 2 (parasites mostly known to feed on echinoderms, bryozoans, cnidarians, or sponges with stylet-like mandibles and siphon for sucking body juices or tissues) are secondary consumers, and type 3 (parasites with a cutting, boring siphon) are both secondary and tertiary consumers.

2.5. Ecological indices and statistical analyses

Cumulative species–effort curves were generated for the two sampling locations EPR and MAR. The cumulative sampling effort, which means the number of identified individuals, was plotted against the cumulative number of identified species. For average k -dominance curves, showing the degree of heterogeneity and dominance patterns within the EPR and MAR samples, the relative abundance of each species was plotted against the decreasing rank of dominating species. The same procedure was carried out with genera.

In addition to simple species richness in a sample, a count of Margalef’s species richness (d) was estimated ($d = (S - 1) / \ln N$; $S = \text{number of species}$, $N = \text{number of individuals per sample}$; Margalef, 1958). Other diversity indices also take into account species richness and the abundance of species. A high Fishers α -value indicates a large number of rare species, while Simpson’s diversity ($1 - \lambda$) gives the probability that 2 haphazardly selected individuals

from a sample belong to different species. Shannon–Wiener's index of diversity (H'_{\log_e} and H'_{\log_2} ; for comparisons both values were calculated) takes into account the species richness and the proportion of each species within the community, with low H' indicating a low diversity (Hayek and Buzas, 1997). Pielou's evenness (J') indicates how evenly individuals are distributed among different species. When all species occur in similar proportions, the evenness value is one (Pielou, 1975). All these diversity and evenness indices were also calculated for genera. To make data comparable with nematode studies from hydrothermal vents and deep-sea sediments, nematode diversity and evenness were also calculated on species and genus level.

Hierarchical clustering and non-metric, multi-dimensional scaling (MDS) techniques were used to compare communities between the two mussel aggregations. The similarity matrices for cluster and MDS analysis were generated using Bray-Curtis similarity (Bray-Curtis, 1975) calculated from square-root transformed, standardized abundance data. The square-root transformation ensures that highly abundant species do not dominate the analysis and that both very abundant and less common species contribute to the similarity matrix (Clarke and Warwick, 2001). Similarity percentage (SIMPER) analysis was used in order to see which species were responsible for similarities/dissimilarities between sites. Analysis of similarity (ANOSIM) was carried out to test whether there is a significant difference in community structure between the two sites. All univariate indices and multivariate measures were performed using the PRIMER v5 package (Plymouth Marine Laboratory; Clarke and Gorley, 2001).

Several statistical tests (G -test, t -test) were done to test significant differences in abundance, species richness, diversity, and evenness between sites. The null-hypothesis was formulated that the two mussel aggregations are equal in terms of abundance, species richness and diversity.

3. Results

3.1. Abundance and biomass of meiobenthos

The three MAR samples contained more mussels (19.3 ± 2.9), a greater mussel volume (3800 ± 250 ml), and also more sediment (13.1 ± 1 ml) than the three EPR samples (9.3 ± 0.6 mussels; 2700 ± 150 ml mussel volume; 8.2 ± 1.2 ml sediment) (Table 1). Despite the

fact that the two mussel aggregations differed in abundance and average size of mussels and the proportional volume of mussels, sediment, and water content, the abundance of meiobenthos was not significantly different between sites (G -test: 17.35, d.f. = 5, $p > 0.05$). The abundance at MAR was 43 ± 5 individuals per 10 cm^2 , while at EPR it was 32 ± 4 individuals per 10 cm^2 (Table 2; Fig. 2). Also, when related to a standardized volume of 1000 ml mussel volume, the overall abundance of meiobenthos at MAR (601 ± 37 individuals per 1000 ml) was similar to that at EPR mussel bed (EPR 580 ± 90 individuals per 1000 ml; Table 2). Meiobenthic biomass was estimated to be approximately three times greater at EPR (2.7 ± 0.25 mg per 10 cm^2) than at MAR (1.0 ± 0.13 mg per 10 cm^2).

3.2. Composition of meiobenthos

In approximately 4000 counted specimens from EPR and MAR sites, 24 species (belonging to 20 genera and 12 families) were discovered in EPR samples, in contrast to 15 species (belonging to 13 genera and 11 families) in MAR samples. We identified 9 nematode species, 14 copepod species and 1 ostracod species at EPR. At MAR, 7 species were nematodes, 6 were copepods, and one species each an ostracod and a mite. All nematode species were new to science. However, they belong to well-known genera occurring in a variety of habitats from shallow waters to the deep sea. Except for two undescribed harpacticoid species of *Halectinosoma*, all other identified copepod species have been described (Table 3). Two planktonic copepod species, *Isaacsicalanus paucisetus* Fleminger, 1983 (less than 1% of total meiofauna at both sites) and *Oncaea praeclara* Humes, 1988 (less than 1% of total meiofauna at EPR) were excluded from the study. The nematode genera *Thalassomonhystera*, *Megadesmolaimus*, *Anticoma*, *Chromadorita*, and *Leptolaimus* and the copepod genera *Aphotopontius*, *Bathylaophonte*, and *Halectinosoma* were found at both sites, with different species at each site. The copepod genus *Aphotopontius* was represented with 4 species at EPR and with 3 species at MAR. Additionally, two species belonging to the copepod genus *Ceuthocetes* were found at EPR.

The dominance of the two most abundant taxa of meiobenthos, nematodes and copepods, was remarkably different between the two sites. At MAR, nematodes dominated ($63 \pm 19\%$) followed by copepods ($35 \pm 4\%$). At EPR, copepods ($85 \pm 2\%$)

Table 3

Identification of permanent meiobenthos associated with hydrothermal vent *Bathymodiulus* beds at East Pacific Rise (EPR) and Mid-Atlantic Ridge (MAR)

Copepoda	Site	F. type	Nematoda	Site	F. type
Ord. SIPHONOSTOMATOIDA			Ord. MONHYSTERIDA		
Fam. Dirivultidae Humes and Dojiri, 1981			Fam. Monhysteridae De Man, 1876		
Gen. Aphotopontius Humes, 1986			Monhysteridae sp. 1	EPR	PC
<i>Aphotopontius arcuatus</i> Humes, 1986	EPR	PC	Gen. <i>Thalassomonhystera</i> Jacobs, 1987		
<i>Aphotopontius atlanteus</i> Humes, 1986	MAR	PC	<i>Thalassomonhystera</i> sp.1	EPR	PC
<i>Aphotopontius forcipatus</i> Humes, 1987	MAR	PC	<i>Thalassomonhystera</i> sp. 2	MAR	PC
<i>Aphotopontius limatulus</i> Humes, 1987	EPR	PC	Fam. Xyalidae Chitwood, 1951		
<i>Aphotopontius mammilatus</i> Humes, 1987	EPR	PC	Gen. Theristus Bastian, 1865		
<i>Aphotopontius rapunculus</i> Humes and Segonzac, 1998	EPR	PC	<i>Theristus</i> sp.1	EPR	PC
<i>Aphotopontius temperatus</i> Humes, 1997	MAR	PC	Fam. Linhomoeidae Filipjev, 1922		
Gen. Ceuthocetes Humes, 1986			Gen. Megadesmolaimus Wieser, 1954		
<i>Ceuthocetes acanthothrix</i> Humes, 1987	EPR	PAR	<i>Megadesmolaimus</i> sp.1	EPR	PC
<i>Ceuthocetes aliger</i> Humes and Dojiri, 1980	EPR	PAR	<i>Megadesmolaimus</i> sp.2	MAR	PC
Gen. Exrima Humes, 1987			Gen. Paralinhomoeus De Man, 1907		
<i>Exrima dolichopus</i> Humes, 1987	EPR	PC	<i>Paralinhomoeus</i> sp.1	EPR	PC
Gen. Nilva Humes, 1987			Fam. Diplopeltidae Filipjev, 1918		
<i>Nilva torifera</i> Humes, 1987	EPR	PAR	Gen. Araeolaimus De Man, 1888		
Gen. Rhogobius Humes, 1987			<i>Araeolaimus</i> sp.1	MAR	PC
<i>Rhogobius contractus</i> Humes, 1987	EPR	PC	Gen. <i>Diplopeltula</i> Gerlach, 1950		
Gen. Rimipontius Humes, 1996			<i>Diplopeltula</i> sp.1	MAR	PC
<i>Rimipontius mediospinifer</i> Humes, 1996	MAR	PC	Ord. ENOPLIDA		
Gen. Scotocetes Humes, 1987			Fam. Anticomidae		
<i>Scotocetes introrsus</i> Humes, 1987	EPR	PC	Gen. Anticoma Bastian, 1865		
Gen. Stygiopontius Humes, 1987			<i>Anticoma</i> sp.1	EPR	PC
<i>Stygiopontius sentifer</i> Humes, 1987	EPR	PC	<i>Anticoma</i> sp.2	MAR	PC
Fam. Ecbathyriontidae Humes, 1987			Ord. CHROMADORIDA		
Gen. Ecbathyrionidae Humes, 1987			Fam. Chromadoridae Filipjev, 1919		
<i>Ecbathyrion prolificauda</i> Humes, 1987	EPR	PC	Gen. Chromadorita Filipjev, 1919		
Ord. HARPACTICOIDA			<i>Chromadorita</i> sp.1	EPR	PC
Fam. Laophontidae Scott, 1910			<i>Chromadorita</i> sp.2	MAR	PC
Gen. Bathylaophonte Lee and Huys, 1999			Fam. Cyatholaimidae Filipjev, 1918		
<i>Bathylaophonte azorica</i> Lee & Huys, 1999	MAR	? PC	Gen. Paracanthonchus Micoletzky, 1924		
<i>Bathylaophonte pacifica</i> Lee and Huys, 1999	EPR	? PC	<i>Paracanthonchus</i> sp.1	EPR	PC
Fam. Ectinosomatidae Sars, 1903			Fam. Leptolaimidae Örley, 1880		
Gen. Halectinosoma			Gen. Leptolaimus De Man, 1876		
Halectinosoma sp. 1	EPR	? PC	<i>Leptolaimus</i> sp.1	EPR	PC
Halectinosoma sp. 2	MAR	? PC	<i>Leptolaimus</i> sp.2	MAR	PC
Halacaroida			Ostracoda		
Halacarid not ident. sp. 1	MAR	PAR	Ostracoda not ident.sp.1	EPR	PC
			Ostracoda not ident. sp. 2	MAR	PC

Classification to feeding types (F. type) include: primary consumers (PC) and parasites (PAR).

were more abundant than nematodes ($6 \pm 2\%$). Ostracods were rare at both sites. Mites were rare at MAR and were absent at EPR. The relative abundances of nematode and copepod species for each site are listed in Table 4. The vent endemic copepod family Dirivultidae dominated the EPR samples. They made up $\sim 70\%$ of the meiobenthic community. *Aphotopontius mammilatus* was the most abundant copepod species in the

EPR samples, making up on average 15.8% of the total abundance, followed by *Rhogobius contractus* (10.8%), *Aphotopontius rapunculus* (10.7%), and *Scotocetes introrsus* (9.9%). An additional 7 species of Dirivultidae contributed to 23.5% of the total abundance, and the remaining 3.8% were harpacticoid copepods. The most abundant nematode at EPR was a *Thalassomonhystera* species, which contributed 7.6% of the total meiobenthic

Table 4

Relative abundance of permanent meiobenthic species (mean % of total \pm standard deviation SD; data were arcsine transformed) of East Pacific Rise (EPR) samples ($n = 3$) and Mid-Atlantic Ridge (MAR) samples ($n = 3$)

EPR	Mean % \pm SD	MAR	mean % \pm SD
Copepoda		Copepoda	
<i>Aphotopontius mammilatus</i>	15.8 \pm 5.6	<i>Aphotopontius atlanteus</i>	24.3 \pm 9.6
<i>Rhogobius contractus</i>	10.8 \pm 5.2	<i>Aphotopontius forcipatus</i>	11.1 \pm 3.5
<i>Aphotopontius rapunculus</i>	10.7 \pm 3.3	<i>Halectinosoma</i> sp.2	3.5 \pm 2.3
<i>Scotocetes introrsus</i>	9.9 \pm 1.8	<i>Aphotopontius temperatus</i>	1.7 \pm 0.7
<i>Ceuthocetes aliger</i>	6.8 \pm 2.9	<i>Rimipontius mediospinifer</i>	1.4 \pm 1.1
<i>Nilva torifera</i>	6.8 \pm 2.3	<i>Bathylaophonte azorica</i>	0.4 \pm 0.2
<i>Ecbathyrion prolixicauda</i>	5.9 \pm 3.0		
<i>Aphotopontius limatulus</i>	3.7 \pm 2.4		
<i>Halectinosoma</i> not ident. sp.1	2.5 \pm 1.1		
<i>Exrima dolichopus</i>	2.4 \pm 1.7		
<i>Ceuthocetes acanthotrix</i>	2.3 \pm 1.1		
<i>Aphotopontius arcuatus</i>	1.3 \pm 0.1		
<i>Bathylaophonte pacifica</i>	1.3 \pm 1.1		
<i>Stygiopontius sentifer</i>	0.2 \pm 0.3		
Nematoda		Nematoda	
<i>Thalassomonhystera</i> sp.1	7.6 \pm 3.6	<i>Thalassomonhystera</i> sp.2	47.2 \pm 9.6
Monhysteridae sp. 1	2.6 \pm 2.2	<i>Anticoma</i> sp.2	2.6 \pm 1.2
<i>Theristus</i> sp.1	2.4 \pm 1.7	<i>Diplopetula</i> sp.1	2.6 \pm 2.2
<i>Paralinhomoeus</i> sp.1	1.4 \pm 0.4	<i>Chromadorita</i> sp.2	1.3 \pm 0.6
<i>Paracanthochus</i> sp.1	1.3 \pm 0.1	<i>Megadesmolaimus</i> sp.2	1.3 \pm 0.4
<i>Megadesmolaimus</i> sp.1	1.2 \pm 0.3	<i>Araeolaimus</i> sp.1	1.2 \pm 0.3
<i>Anticoma</i> sp.1	1.1 \pm 0.5	<i>Leptolaimus</i> sp.2	1.1 \pm 0.5
<i>Leptolaimus</i> sp. 1	0.9 \pm 0.8		
<i>Chromadorita</i> sp. 1	0.8 \pm 0.5		
Ostracoda		Ostracoda	
<i>Ostracoda</i> not ident. sp.1	0.3 \pm 0.1	<i>Ostracoda</i> not ident. sp. 2	0.01 \pm 0.0
		Halacaroida	
		<i>Halacarid</i> not ident. sp. 2	0.3 \pm 0.0

community. The other 8 nematode species at EPR made up a total of 11.7%.

In contrast to the EPR mussel bed, Dirivultidae made up only 38.5% of the whole meiobenthic community at the MAR mussel bed. Here, this family was dominated by *Aphotopontius atlanteus* (24.3%), followed by *Aphotopontius forcipatus* (11.1%). The remaining copepod species only contributed 7%. *Thalassomonhystera* sp. 2 represented 47.2% of the entire community and was clearly the dominant species. The other 6 nematode species accounted for 10.1%. Mites and ostracods made up less than 0.5% at each site (Table 4).

Copepod and nematode sex ratios were biased in favor of females at both sites. The female:male copepod ratio was 1.3:1 at EPR and 3.1:1 at MAR. More than twice as many female nematodes than males were found at EPR (2.6:1), while at MAR the ratio was 1.8:1.

3.3. Diversity and community structure of meiobenthos

Species–effort curves, calculated using the cumulative number of species (Fig. 3A), reached an asymptote, which indicates that the majority of abundant species were sampled and represented in this study.

The species-level k -dominance curves for EPR and MAR did not overlap indicating that diversity was higher and dominance by a single species also higher, at EPR than at MAR (Fig. 4A). The same held true for genera (Fig. 4B). Species richness was higher at EPR (24 species) than at MAR (15 species). Shannon–Wiener $H_{\log e}$ was also significantly higher at EPR than at MAR (G -test: 2350, d.f. = 5, $p < 0.05$; Table 5A). The same held true at the genus level (G -test: 1470, d.f. = 5, $p < 0.05$; Table 5B). Furthermore, the same trend was found

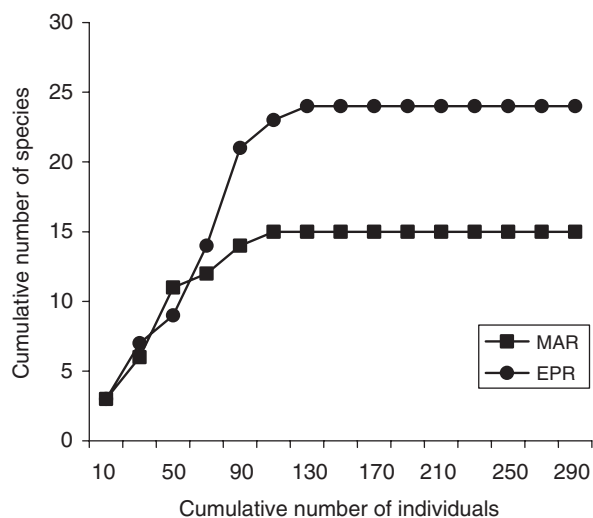


Fig. 3. Species effort curves for permanent meiobenthos associated with *Bathymodiolus* mussel beds at Mid-Atlantic Ridge (MAR) and East Pacific Rise (EPR); effort based on cumulative number of individuals. Others include ostracods, mites, not further identified juveniles of polychaetes and molluscs, nauplii of crustaceans, and planktonic copepods.

for Margalef's d , Fisher's α , Simpson's $1-\lambda'$, Shannon–Wiener H'_{\log_2} , and Pielou's J' (Table 5A). Therefore, the meiobenthic community at EPR was significantly more diverse and individuals were more evenly distributed among species compared to the community at MAR. Nematode Shannon–Wiener H'_{\log_e} diversity index was higher at EPR than at MAR (G -test: 1237, d.f. = 5, $p < 0.05$), and this was also seen for evenness. Because each genus found was represented only by one species at any site, species and genera indices were identical (Table 5C).

Hierarchical cluster analyses were conducted to determine the degree of similarity. SIMPER analysis revealed a similarity of 79% between the three EPR samples, a similarity of 92.9% between the three MAR samples and a dissimilarity of 100% between the two sites, as there were no shared species between the two sites, i.e. there were no species in common between EPR and MAR (Fig. 5A). Within sites, similarity of genera was 77.2% between EPR samples, 82.4% between MAR samples and the dissimilarity was 65.9% between sites (Fig. 5B). SIMPER revealed the following species-level contributions to the similarity of the three samples: *A. mammilatus* (average of 12.5%), *S. introrsus* (12.2%), *A. rapunculus* (11.2%), and the nematode species, *Thalassomonhystera* sp. 1 (8.6%) contributing to the similarity of the three samples.

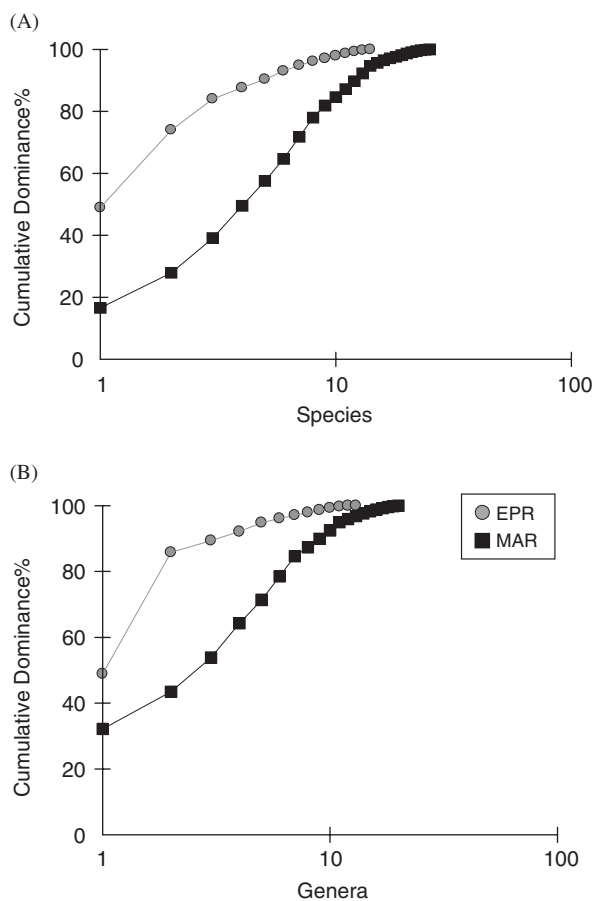


Fig. 4. K -dominance curves on species (A) and on genus (B) level data for East Pacific Rise (EPR) and Mid-Atlantic Ridge (MAR) samples, calculated for permanent meiobenthos. Abundances of species (A) and genera (B) were plotted against species viz. genera ranks.

At MAR, *Thalassomonhystera* sp. 2 contributed with an average of 40.2%, followed by *A. atlanteus* (26.4%) and *A. forcipatus* with (11.1%) to the similarity of the three samples. MDS ordination also points out the clear separation and the differences of the two mussel aggregations, which is more evident at the species level (Fig. 6A) than at the genus (Fig. 6B) level. However, ANOSIM did not show significant differences in the community structures between the two sites, which is due to the limited number of samples ($R = 1$, $p < 0.1$).

3.4. Trophic structure

Primary consumers, mostly deposit feeders, comprised more than 95% of the total meiobenthos at the EPR and MAR, followed by parasitic copepods

Table 5
Univariate calculations for diversity and evenness of permanent meiobenthos on species (A) and genus (B) level for Mid-Atlantic Ridge (MAR) and East Pacific Rise (EPR) samples ($n = 3$)

	MAR ($n = 3$)	EPR ($n = 3$)
(A)		
Species richness	15	24
Margalef d	1.85	3.26
Fisher α	2.22	4.29
Simpson $1-\lambda'$	0.69	0.91
Shannon H'_{\log_2}	2.26	3.81
Shannon H'_{\log_e}	1.57	2.64
Pielou J'	0.58	0.83
(B)		
Genus richness	13	20
Margalef d	1.59	2.70
Fisher α	1.88	3.44
Simpson $1-\lambda'$	0.62	0.85
Shannon H'_{\log_2}	1.85	3.126
Shannon H'_{\log_e}	1.28	2.26
Pielou J'	0.50	0.76
(C)		
Species richness	7	9
Margalef d	0.84	1.54
Fisher α	0.98	1.99
Simpson $1-\lambda'$	0.45	0.74
Shannon H'_{\log_2}	1.45	2.41
Shannon H'_{\log_e}	1.02	1.67
Pielou J'	0.53	0.76

Calculations were also done for nematodes on species and genus (C) level for MAR and EPR samples.

and mites. All nematodes and the majority of copepod individuals (80% of Dirivultidae), were primary consumers at both sites. The copepod parasites such as *Ceuthocetes* species and *Nilva torifera* only made up 20% of the copepod community. Predators were absent in all samples.

4. Discussion

4.1. Meiobenthic community structure of EPR and MAR mussel beds

This study of two mussel beds from geographically distant locations at the EPR and MAR is the first attempt to describe the community and trophic structure of permanent, invertebrate meiobenthos at vents. Both communities can be characterized as epibenthic hard substrate communities, exhibiting low species richness (24 species at EPR, 15 species at MAR), low diversity (H'_{\log_e} 2.6 at EPR, H'_{\log_e} 1.6 at MAR), and low abundance (32 ± 4 individuals per

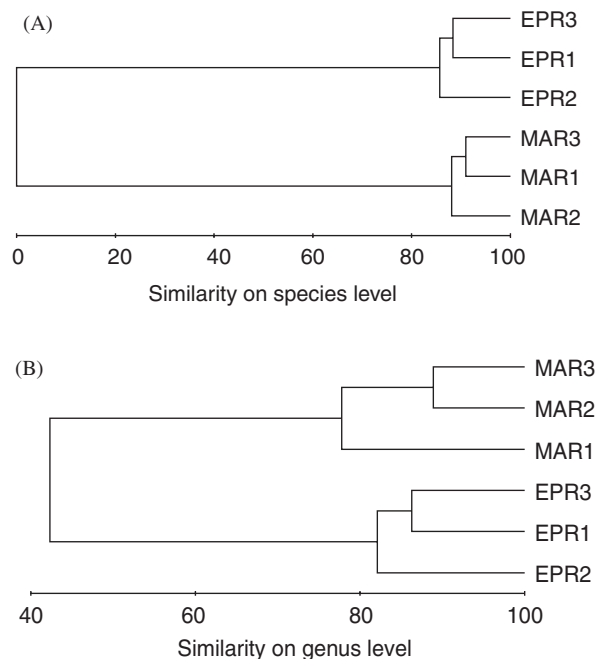


Fig. 5. Hierarchical cluster diagram for group average linking based on Bray-Curtis similarities of species (A) and genera (B) for East Pacific Rise (EPR1–EPR3) and Mid-Atlantic Ridge (MAR1–MAR3) samples, calculated for permanent meiobenthos. Abundance data were standardized to numbers of individuals per 10 cm^2 and square root transformed.

10 cm^2 at EPR, 43 ± 5 individuals per 10 cm^2 at MAR). However, species richness and diversity were higher at EPR (24 species, H'_{\log_e} 2.6) than at MAR (15 species, H'_{\log_e} 1.6). Additionally the proportion of each species was more even in the EPR mussel bed community compared with the MAR community, which was highly dominated by two abundant species. The nematode *Thalassomonhystera* sp. 2 accounted for about half of the individuals and the copepod *A. atlanteus* was about one fourth; the remaining 13 species together account for about one fourth of the total individuals. Species richness of macrobenthos was also found to be higher at EPR than at MAR mussel beds (40 species, Buckfield, EPR (Dreyer et al., 2005); 23 species, Moose, MAR (Turnipseed et al., 2004)). Diversity indices, however, indicated that the distribution of individuals among macrobenthic species was similar (Buckfield, EPR H'_{\log_e} 1.5–1.7, Dreyer et al., 2005; Moose, MAR H'_{\log_e} 1.8, Turnipseed et al., 2004).

Explanations for differences in the structure of animal communities associated with mussel aggregations in the Pacific and the Atlantic are not obvious. It has been hypothesized that differences in

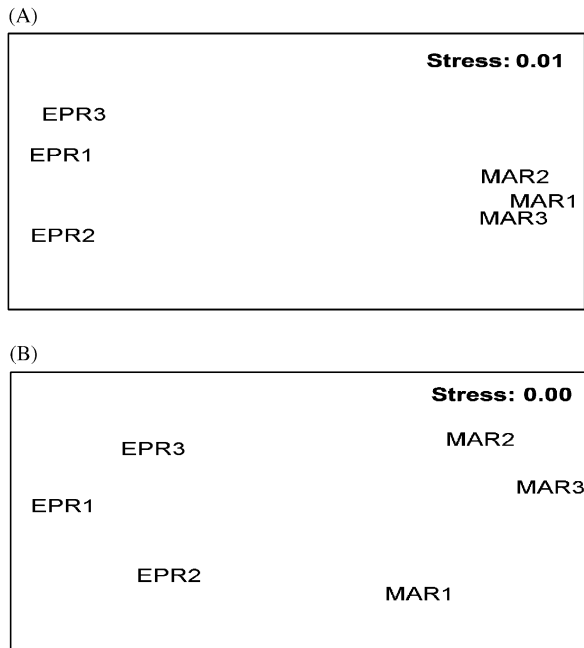


Fig. 6. MDS plots based on Bray-Curtis similarities of species (A) and genera (B) for East Pacific Rise (EPR1–EPR3) and Mid-Atlantic Ridge (MAR1–MAR3) samples. Abundance data were standardized to numbers of individuals per 10 cm² and square root transformed.

ages of the oceans, spreading rates, spatial distribution and persistence of vent fields, depth, and productivity might cause the different macrobenthic community structures at hydrothermal vent mussel beds (Van Dover, 2002, 2003). The same may hold true for the differences in meiobenthic communities. Geological activities (volcanism, tectonics) are greater on fast-spreading axes (EPR) than on slow-spreading axes (MAR), resulting in greater disturbances at EPR hydrothermal vent systems (Van Dover, 2000). These higher disturbances, also according to the Intermediate Disturbance Hypothesis (Connell, 1987) and the Spatial Temporal Mosaic Hypothesis (Grassle, 1989), may result in increasing species diversity (Juniper and Tunnicliffe, 1997, Van Dover, 2002, 2003). Fast-spreading axes (EPR) also exhibit a different spatial distribution and persistence of vent fields compared with slow-spreading axes (MAR). Distances between active zones are greater at slow than at fast spreading ridges, and thus exchanges between populations may be less frequent at the former, and the probability of extinction even greater, resulting in lower overall diversity where vents are far apart (Van Dover, 1995, 2000; Juniper and Tunnicliffe,

1997; Desbruyères et al., 2001). These different factors, disturbances on small and large scales, may produce differences in local species composition and distribution at the two vent mussel beds.

A comparison of the nematode community structure of mussel beds reveals that the communities of the EPR and MAR mussel beds, where mussels grew on basalt, were less diverse (H'_{\log_e} 1.7 EPR, H'_{\log_e} 1 MAR; this study), and lower in number of species, than those from the West Pacific, where mussels grew on sediment (H'_{\log_e} 3.4; Vanreusel et al., 1997). Greater meiofaunal diversity in sediment-hosted mussel-bed habitats may result from greater habitat heterogeneity in these systems compared to mussel-bed habitats on bare basalt.

Copepod diversity was greater in mussel beds (this study), where overall physico-chemical conditions are relatively moderate, than in tubeworm aggregations from Juan de Fuca Ridge (Tsurumi et al., 2003), where temperatures and concentrations of hydrogen sulfide are higher (Tsurumi and Tunnicliffe, 2003). While these data may point to an inverse correlation between diversity and vent flux, the data are too scarce to draw any general conclusions.

The meiofauna of other sulfidic habitats, such as the ‘thiobios’ of sulfidic sediments, shallow-water vents, or cold seeps, appear to have no strong affinities to the deep-sea vent meiofauna of mussel beds, despite the presence of reducing chemicals and hypoxia. Vent mussel bed meiobenthos was mainly composed of endemic Dirivultidae and species of generalistic nematodes known from many other shallow-water and deep-sea habitats. The ‘thiobios’ is characterized by typical taxa, such as nematodes, gnathostomulids and platyhelminths (especially Acoela-Solenophilomorphidae and Catenulida-Retronectidae), gastrotrichs, and ciliates, which are specially adapted to sediments with high amounts of sulfide and little oxygen (Fenchel and Riedl, 1970; Boaden and Platt, 1971; reviewed in Ott et al., 2004). For example, nematodes belonging to Stilbonematinae with ectosymbiotic bacteria are usually a prominent component of this community, also occurring at shallow-water seeps (Ott and Novak, 1989; Ott et al., 1991; in Ott et al., 2004, see Levin, 2005) and are known from shallow-water vents and seeps (e.g. Kamenev et al., 1993; Thiermann et al., 1994) but are so far absent at deep-sea vents. In contrast, the deep-sea seep meiobenthic community is mostly an unspecialized assemblage, with Dirivultidae lacking or scarce

(Shirayama and Ohta, 1990; Humes and Segonzac, 1998; Heptner and Ivanenko, 2002) and usually also generalistic nematodes (see Levin, 2005).

4.2. Meiobenthic abundance at EPR and MAR mussel beds

Macrobenthic hydrothermal vent animals occur in high abundances, usually numerically dominated by a small number of species (Van Dover and Trask, 2000; Van Dover, 2002, 2003; Tsurumi and Tunnicliffe, 2003; Turnipseed et al., 2003, 2004; Dreyer et al., 2005). This stands in contrast to the low abundance of meiobenthic animals (this study, Dinét et al., 1988). Meiofauna from vent sediments at the Guaymas Basin were also scarce ($<1\text{--}80$ individuals per 10 cm^2 ; Dinét et al., 1988). Within an area of 10 cm^2 less than 40 individuals live at the mussel beds at EPR and MAR (this study). The relative abundance of the two most prominent taxa, nematodes and copepods, was different between the MAR and EPR mussel bed and this was also expressed in the different average biomasses found. Within 10 cm^2 , an average of 27 copepod individuals was counted at EPR but only 16 individuals at MAR. Even more pronounced was the difference in nematode abundance, where on average only 6 individuals per 10 cm^2 at EPR were in contrast to 28 individuals per 10 cm^2 found at MAR.

The abundance of meiobenthos at deep-sea vents, albeit inferred from the limited data set available so far, was lower than in the majority of other meiobenthic shallow water and deep-sea communities. Average abundance values for sediment communities were estimated between 1000 and 2000 individuals per 10 cm^2 (in Giere, 1993; Table 6). In deep-sea clays and oozes, abundances ranged between 4 and 6378 individuals per 10 cm^2 (see Soltwedel, 2000); densities below 100 individuals per 10 cm^2 were the exception rather than the rule in this environment (see Soltwedel, 2000; Danovaro et al., 2000, 2002; Gambi et al., 2003). A general trend of decreasing abundance with increasing water depth, reflecting decrease in food-availability and reduction of sediment grain size down to silt has been reported (see Soltwedel, 2000). The deep-sea seep meiobenthic communities in the Gulf of Mexico, the Santa Barbara Channel, and the Barbados prism also included more than 100 individuals per 10 cm^2 , reaching densities larger than 2000 individuals (e.g. Palmer et al., 1988; Montagna et al., 1989; Montagna and Harper,

1996; Olu et al., 1997; Table 6). Meiobenthic densities from deep-sea mud volcanoes or gas hydrate fields exceeded more than 900 individuals per 10 cm^2 (Gutzmann, 2003; Soltwedel et al., 2005). Even in rarely studied hard substrate communities from shallow waters, meiofaunal abundances exceeded 100 individuals per 10 cm^2 , but always were much lower than adjacent soft bottom communities (Danovaro and Fraschetti, 2002; Atilla et al., 2003).

The similar low abundances at MAR and EPR mussel beds were unexpected in this deep-sea environment with in situ primary production. The synthesis of organic matter by free-living microbes is thought to be important at vents in general, providing food for the grazing and deposit-feeding primary consumers, but remains so far unquantified in mussel beds (see Tunnicliffe et al., 2003). Measurements of primary production rates or quantities of organic material were outside the scope of this study. However, from the large abundance of macrobenthos associated with mussel beds (Van Dover and Trask, 2000; Van Dover, 2002, 2003; Turnipseed et al., 2003, 2004), it can be inferred that organic matter is present in considerable quantities. Macrobenthos abundance values, using the same samples as for this study, were as high as 126 ± 22 individuals per 1000 ml at MAR (Turnipseed et al., 2004) and 385 ± 142 individuals per 1000 ml at EPR (Dreyer et al., 2005), while the corresponding meiobenthic abundances were 601 ± 367 individuals per 1000 ml at MAR and 580 ± 90 individuals per 1000 ml at EPR.

We hypothesize that the abundance of meiobenthos at hydrothermal vents is strongly influenced by the macrobenthos. A large number of macrobenthic deposit feeders and grazers unselectively feed on the particulate organic material accumulated between mussel shells thus potentially diminishing also the meiobenthic fauna. Also smaller and/or juvenile macrofauna predators may account for the scarcity of meiofauna. For example, the predatory polychaete *Ophryotrocha akessoni* Blake, 1985 is highly abundant at the EPR mussel bed (Dreyer et al., 2005). All these top-down controlling processes seem reasonable but remain to be tested.

5. Conclusion

Mussel beds provide additional hard substrate with their shells, thus increasing habitat complexity. Mussels also add to the organic food supply available to meiofauna by secretions and faeces.

Table 6

Comparison of meiobenthic and nematode abundances (individuals per 10 cm²) from chemosynthetic deep sea habitats (hydrothermal vents, seeps and whale falls) and soft-sedimented deep-sea

Location	Individuals per 10 cm ²	References
<i>Hydrothermal vents</i>		
EPR 11°N: total meiofauna	32 ± 4	This study
MAR 23°N: total meiofauna	43 ± 5	
<i>Guaymas Basin</i>		
Hydrothermal vent site: total meiofauna	1–81	Dinet et al., 1988
“Control” site (non-vent): total meiofauna	170–372	
<i>Cold Seep Barbados, mud Volcano</i>		
Total meiofauna	116–11364	Olu et al., 1997
<i>Petroleum Seep Santa Barbara</i>		
Total meiofauna	800–2500	Palmer et al., 1988
<i>Deep-sea mud volcano</i>		
Bacterial mats: total meiofauna	2902	Soltwedel et al., 2005
Pogonophora field: total meiofauna	985	
Control site (sediment): total meiofauna	1131	
<i>Deep-sea gashydrate field</i>		
Bacterial mats: total meiofauna	794	Gutzmann 2003
Clam field: total meiofauna	826	
Control site (sediment): total meiofauna	1196	
<i>Hydrothermal vents</i>		
EPR 11°N: nematodes	6	This study
MAR 23°N: nematodes	28	
<i>Cold Seep Barbados</i>		
Mud Volcano: nematodes	116–8336	Olu et al., 1997
<i>Santa Cruz Basin</i>		
Around Whale fall (0–9 m): nematodes	12–641	Debenham et al., 2004
Far from Whale fall (+ 30 m): nematodes	2261–5552	
<i>Deep-sea mud volcano</i>		
Bacterial mats: nematodes	2529	Soltwedel et al., 2005
Pogonophora field: nematodes	533	
Control site (sediment): nematodes	731	
<i>Deep-sea gashydrate field:</i>		
Bacterial mats: nematodes	138	Gutzmann, 2003
Clam field: nematodes	435	
Control site (sediment): nematodes	919	

Nevertheless, the potential toxicity of vent emissions, the nature of the substratum (basalt rock rather than soft sediment), and the increased predation pressure and competition by associated macrofauna, may shape the meiobenthic community structure in vent mussel beds. These characteristics have led to the evolution of a vent mussel bed community of generalist nematodes and endemic copepods. This assemblage is not related to any other sulfidic habitat, neither to shallow water, thio bios sediments or shallow water vents, nor to deep-sea cold seeps. Comparisons of macrofaunal

(11°N EPR: Dreyer et al., 2005; 23°N MAR: Turnipseed et al., 2004) and meiofaunal species richness demonstrate that meiobenthos contributes at least 50% to the total macro- and meiofaunal species diversity in vent mussel beds. This highlights the importance of including meiobenthos in estimations of biodiversity and community structure at hydrothermal vents. Further investigations are needed to define patterns of meiobenthic distribution and diversity in order to develop an understanding of various processes of hydrothermal vents.

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