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Meiofaunal diversity and assemblage structure in a shallow-water hydrothermal vent in the Pacific Ocean

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ABSTRACT: Despite their ubiquitous distribution in tectonically active coastal zones, shallow-water vents have been much less explored than deep-sea vents in terms of biodiversity and adaptations to extreme conditions. We investigated the meiofaunal biodiversity and environmental variables at distances of 10, 100 and 200 cm from a shallow-water hydrothermal vent in the equatorial Pacific (Sulawesi, Indonesia). Meiofaunal abundance and the richness of higher taxa increased from the site of fluid-vent emission (where temperatures of the fluids and sediments reached approximately 90°C) to the control sediments (200 cm from the vent, with no sign of effects from the vent fluids). Nematode species richness was also high in the intermediate station, where bottom sediment temperature reached 55°C. These data suggest that some nematode species were able to survive in conditions typically hostile to metazoan life. Gas emissions also influenced the biochemical composition of the sediment organic matter in proximity to the vent and favoured the growth of a large photo- and/or chemo-autotrophic prokaryotic biomass. This biomass represented a potentially important food source for predator/omnivore nematodes and influenced the trophic structure of benthic assemblages. Since the metazoan species found in proximity to the vent were a subset of those inhabiting control sediments, but were characterised by lower abundances, it might be hypothesized that the populations close to the vent are the result of colonization from adjacent areas.

KEY WORDS: Shallow-water hydrothermal vent · Meiofaunal diversity · Extreme environments

INTRODUCTION

Extreme natural environments offer unique opportunities to investigate not only the biological response and adaptation of organisms to extreme conditions (Rothschild & Mancinelli 2001) but also the effect of extreme conditions on biodiversity (Amils et al. 2007). Cold seeps, oxygen minimum zones and hydrothermal vents are extreme environments that strongly select or drive the patterns of the living components found there (species diversity, life strategies), alter classical ecological pathways (altering food webs) and force organisms to find alternative pathways to cope with the hostile environmental conditions encountered there.

Shallow-water hydrothermal vents typically release free gas and hot water, thus creating extreme local conditions. These systems are strongly variable in space and time, and are often ephemeral (i.e. display a short duration ranging from months to decades; Van Dover 1990). Although these systems have been reported from several oceans (including off the coasts of California, New Zealand, Iceland, Japan, Papua New Guinea and Mexico) and from the Mediterranean Sea (Manini et al. 2008), an exact global inventory of the shallow-water vents is lacking and knowledge on such vents is still poor when compared with that on deep-sea hydrothermal vents (Tarasov et al. 2005).

Previous studies showed that the fauna from shallow-water vents are different from those found at deep-sea vents (Tarasov et al. 2005). Deep-sea vents are based on chemosynthetic production, whilst the co-presence of light and geothermal fluids at shallow vents promotes

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both photo- and chemosynthetic primary production. This dualism complicates the identification of the different functional roles of components in these systems (Tarasov et al. 1986, Tarasov 1991, 2006).

Comparisons of macro- and meiofaunal biodiversity in mussel beds associated with deep-sea vents indicate that meiofaunal species richness contributes to at least 50% of the total benthic diversity (Zekely et al. 2006, Copley et al. 2007). Nematode diversity and density in deep-sea sediments north of Fiji were lower in deep-sea vent areas than in the surrounding area (Vanreusel et al. 1997).

Similarly, in the shallow Fumarole Bay, a monocelid turbellarian species characterized by epi-symbiotic bacteria (Bright et al. 2003) was particularly abundant, whereas meiofaunal abundance otherwise decreased. Conversely, in shallow-water hydrothermal vents of the Kraternaya Bight, meiofaunal diversity and abundance were higher than in background sediments (Tarasov et al. 2005). The macrofauna of shallow-vent assemblages represent a subset of the macrofauna of surrounding sediments, with limited diversity and lower abundance (Dando et al. 1995, Thiermann et al. 1997). Some taxa (e.g. solemyid, lucinid and thyasirid bivalves and desmodorid nematodes) develop symbiotic relationships with sulphur-oxidising bacteria, but they are unable to tolerate high temperatures, as well as the sulphides and metals released by vent emissions (Dando et al. 1995, Thiermann et al. 1997, Melwani & Kim 2008).

Here, we investigated the effects of an active shallow-water hydrothermal vent in the Pacific Ocean on benthic biodiversity and on the associated potential food sources.

MATERIALS AND METHODS

Study site and sampling strategy. The investigated site is part of the Indonesian archipelago (Pacific Ocean). The archipelago is characterized by the presence of 129 volcanoes, responsible for gas emissions from the sea bottom in several coastal areas. The investigated site was located in the Strait of Lembeh, between Sulawesi and the Moluccas Sea, in the region north of Sulawesi Island (1° 26′ 12.00″ N, 125° 12′ 15.01″ E). The vent was at a depth of 3 m, and the fluid temperature from the caldera was 90°C (gas flux 0.809 m^3 min^{-1}; Fig. 1). The caldera was approximately 50 cm in diameter and 70 cm high. The caldera's walls were very compact and made sediment coring impossible. They had coloured bands indicating prokaryotic (likely chemo-autotrophic) colonization. The sampling strategy was aimed at investigating the influence of the vent on the sediments in close proximity of the emission. Sediments were sampled by SCUBA divers at different distances from the seepage: inside the caldera's wall

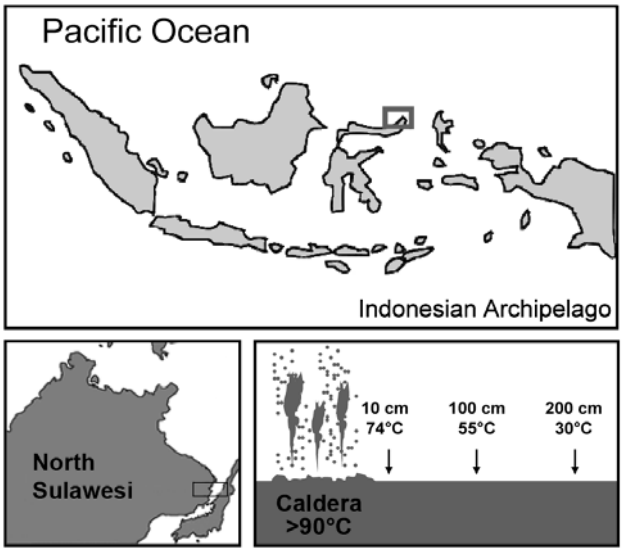

Fig. 1. Sampling area and schematic representation of locations of sampling stations at different distances from the seepage (i.e. caldera)

(sampled with a sterile spatula for biochemical analyses, as the walls were solid and could not host interstitial fauna), and at 10, 100 and 200 cm (control site) away from the vent (for all of the variables) on soft substrates using Plexiglas corers (3.7 cm diameter) down to a depth of 15 cm. Since the vent emission did not show any current-forced direction, 6 independent replicate cores were randomly collected along multiple transects, at increasing distances from the vent. For the analyses of the biochemical composition of organic matter in the sediment, the first centimetre of each of 3 replicate corers was frozen at –20°C until analysis. For meiofaunal analyses, 3 sediment cores for each station were preserved in buffered 4% formalin solution and stained with Rose Bengal (0.5 g l^{-1}).

Environmental and biochemical variables. Temperature, pH and salinity were measured using a portable probe model HD 8705 (Delta Ohm and OxyGuard). Chlorophyll *a* (chl *a*) and phaeopigment concentrations were determined according to Lorenzen & Jeffrey (1980). Pigments were extracted (12 h at 4°C in the dark) from triplicate sediment samples (about 1 g) each using 3 to 5 ml of 90% acetone. Extracts were analysed fluorometrically as such to estimate chl *a*, and, after acidification, with 200 µl 0.1 N HCl to estimate phaeopigments. Concentrations are reported as micrograms per gram dry weight. Total phytopigments were defined as the sum of chl *a* and phaeopigments. Analyses were performed in 3 replicates on about 1 g of sediment for each sediment sample. Protein, carbohydrate and lipid sediment contents were analysed spectrophotometrically according to Pusceddu et al. (in press), and concentrations were expressed as bovine serum

albumin, glucose and tripalmitine equivalents, respectively. For each biochemical assay, blanks were obtained using pre-combusted sediments (450°C for 4 h). All analyses were performed in 3 replicates on about 1 g of sediment for each sediment sample. Carbohydrate, protein and lipid sediment contents were converted into carbon equivalents using the conversion factors of 0.40, 0.49 and 0.75 µg C μg^{-1}, respectively, and their sum was defined as the biopolymeric organic carbon (Fabiano et al. 1995).

Nematode biodiversity. All intact nematodes extracted with the rest of the meiofauna from the sediments (see following subsection) were identified at species level, except at 200 cm, where only a subset of ca. 300 ind. was identified. For the analysis of nematode biodiversity, all specimens (from the 3 replicates) were separated and mounted on slides following the formalin-ethanol-glycerol technique described by Seinhorst (1959) to prevent dehydration. Nematodes were identified to species level (whenever possible, due to the presence of several unknown species) according to the recent literature dealing with new nematode genera and species. Species diversity (H', using log-base 2) was measured by the Shannon-Wiener information function and evenness was measured as J' (Pielou 1975). Species richness (SR) was calculated as the total number of species collected at each station; the Margalef index (D) was estimated as $D = (S - 1)/\ln N$, where S is the number of species and N is the number of individuals in the sample (Margalef 1958). Moreover, at each site, the species-abundance data were converted into rarefaction diversity indices (Sanders 1968, as modified by Hurlbert 1971). The expected number of species for a theoretical sample of 51 specimens, ES(51), was selected. The β-diversity (i.e. turnover diversity) was estimated through SIMPER analyses (Gray 2000). A ranked matrix of Bray-Curtis similarities was used as input for this test. To identify colonization strategies of nematodes, the maturity index (MI) was calculated according to the weighted mean of the individual genus scores: $MI = \Sigma v(i)f(i)$, where ν is the c–p value (colonisers–persisters) of genus i as given in the appendix of Bongers et al. (1991) and $f(i)$ is the frequency of that genus. The trophic composition was defined according to Wieser (1953). Nematodes were divided into 4 original groups as follows: (1A) no buccal cavity or a fine tubular one—selective (bacterial) feeders; (1B) large but unarmed buccal cavity—non-selective deposit feeders; (2A) buccal-cavity with scraping tooth or teeth—epistrate or epigrowth (diatom) feeders; and (2B) buccal cavity with large jaws—predators/omnivores. Moens & Vincx (1997) and Moens et al. (1999) recently proposed a modified feeding-type classification based on: (1) microvores, (2) ciliate feeders, (3) deposit feeders sensu strictu, (4) epigrowth feeders, (5) facultative predators and (6) predators. However, in the present study, Wieser's classification was preferred because it allows wider comparison with the available literature. The index of trophic diversity (ITD) was calculated as $ITD = g_1 2 + g_2 2 + g_3 2 \ldots + g_n 2$, where g is the relative contribution of each trophic group to the total number of individuals and n is the number of trophic groups (Gambi et al. 2003). For $n = 4$, ITD ranges from 0.25 (highest trophic diversity, i.e. the 4 trophic guilds account for 25% each) to 1.0 (lowest diversity, i.e. one trophic guild accounts for 100% of nematode density). In the present study, ITD is expressed by 1 – ITD. Nematode biomass was calculated from the biovolume, estimated from at least 100 to 120 specimens $replicate^{-1}$ (>300 specimens $site^{-1}$, whenever possible) using the Andrassy (1956) formula ($V = L \times W^2 \times 0.063 \times 10^{-5}$, in which body length, L, and width, W, are in µm).

Non-nematode meiofauna. Sediment samples were sieved through a 1000 µm mesh, and a 30 µm mesh was used to retain the smallest organisms. The fraction remaining on the latter sieve was re-suspended and centrifuged 3 times with Ludox HS40 (density: 1.31 g cm^{-3}) according to Heip et al. (1985). All meiobenthic animals were counted and classified per taxon under a stereomicroscope. Since the analysis of soft-bodied organisms might be difficult in formalin-preserved samples, some fresh samples were analysed immediately after collection. All soft-bodied organisms from preserved samples were mounted on slides and viewed at 1000× magnification.

Statistical analyses. After testing for the homogeneity of variances using Cochran's test, 1-way analysis of variance (ANOVA) was used to test for differences in all investigated variables between the caldera and the sediments, at a distance of 10, 100 and 200 cm from the vent. When significant differences were encountered, a Tukey's post hoc comparison test (at $\alpha = 0.05$) was also performed to ascertain at which station(s) the investigated parameters were significantly different. ANOSIM analyses, carried out using PRIMER5 software (Plymouth Marine Laboratory; Clarke 1993), were performed to test the presence of statistical differences in the nematode composition among all sampling sites. The PRIMER5 software was also used to build the k-dominance curves and to calculate Bray-Curtis similarities between all sampling sites (for nematodes, data were presence/absence transformed; for meiofauna taxa, data were square-root transformed). The obtained similarity matrix was applied to produce a non-metric, multidimensional scaling 2-dimensional plot (MDS). Average k-dominance curves were generated for the investigated nematode and meiofaunal diversities. The relative abundance of each species/taxon was plotted against the decreasing rank of dominating species/taxa.

RESULTS

Environmental parameters

Fluid temperature measured within the caldera at the vent was >90°C. The temperature in the sediments 10 cm away from the caldera was ca. 74°C, and decreased to 55°C at 100 cm and to ca. 30°C at 200 cm from the vent (Fig. 1). pH values decreased when approaching the vent field, from 8.0 in the control to 6.7 in the fluid emissions.

Chl *a* concentrations were highest in the sediments of the caldera's wall (6.15 ± 0.19 µg g^{-1}) and decreased significantly in surrounding sediments (range: 0.23 ± 0.07 to 3.76 ± 0.80 µg g^{-1}) (Table 1; ANOVA, $p < 0.01$). Phaeopigment concentrations displayed a similar spatial pattern and were always higher than the chl *a* concentrations. The only difference was represented by the low phaeopigment concentrations in the compact sediments of the caldera, where phaeopigment content was ca. 3 times lower than chl *a* concentrations.

Biopolymeric C concentrations in all investigated sediments were low (<0.76 mg C g^{-1}), with lowest values at 10 cm from the vent and highest values at 200 cm (0.76 ± 0.04 mg C g^{-1}; ANOVA, $p < 0.05$). A similar spatial pattern was also observed for proteins and carbohydrates (Table 1). All biochemical components in the sediments of the caldera displayed concentrations higher than in soft sediments at a distance of 10 cm, only with the exception of lipids. In the caldera and in the surrounding soft sediments, proteins were the dominant biochemical class of organic compounds (50 to 61% of biopolymeric C), followed by carbohydrates (26 to 48%) and lipids (2 to 16%) (Fig. 2).

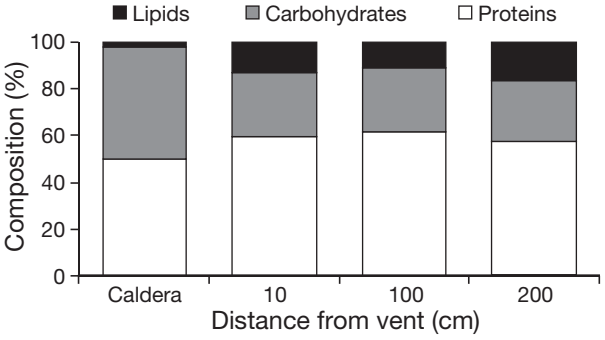

Fig. 2. Biochemical composition of organic matter in the compact sediments inside the caldera and in the soft sediments at increasing distances from the vent

Meiofaunal assemblages and nematode diversity

Meiofaunal abundance ranged from 49.3 ± 8.3 to 3220.6 ± 1179.6 ind. 10 cm^{-2} and increased moving away from the vent (Table 2). Meiofaunal abundance at 200 cm from the vent was significantly higher than in the sediments at 10 cm (Tukey test, $p < 0.01$; Fig. 3). Taxon richness also increased with increasing distances from the vent, ranging from 8 taxa at a distance of 10 cm to 11 taxa at 100 cm and 17 taxa at 200 cm (ANOVA, $p < 0.01$; Table 2). Nematodes, copepods, polychaetes, bivalves, gastrotrichs and nemertines were present at all stations. Ostracods and isopods were present only at 10 and 200 cm from the vent, whilst turbellarians, oligochaetes, tardigrades, tanaidaceans and acarines were present only at 100 and 200 cm from the vent. Finally, kinorhynchs, cumaceans and amphipods were found exclusively at a distance of 200 cm from the caldera (Fig. 4). The biomass of total nematodes significantly increased from 10 to 200 cm (ANOVA, $p < 0.01$; Table 3). The mean individual nematode biomass ranged from 0.06 ± 0.01 to 0.07 ± 0.02 µg C ind.$^{-1}$ and did not show significant differences among sites (ANOVA, not significant [n.s.]; Table 3).

Nematode species richness and the values of Shannon-Wiener, Margalef, Pielou and ES(51) indexes are reported in Table 4. The Pielou index (J) showed significant differences amongst stations, with the highest value at 10 cm from the vent (0.89; Tukey test, $p < 0.01$). Overall, 36 species were identified. The highest number of species (22) was found in the sediments 100 cm away from vent (ANOVA, n.s.), whereas the lowest values were observed at the 10 cm site (11 species). Among all identified families, Enchelidiidae and Ethmolaimidae were encountered only at 100 cm from the vent, while Desmodoridae, Oxystominidae and Sphaerolaimidae were encountered only at a distance of 200 cm (Table 5). At 10 cm from the vent no exclusive

Table 1. Concentrations of phytopigments, biochemical components of organic matter (proteins, carbohydrates and lipids) and biopolymeric carbon (BPC) in the sediment of the sampled stations. DW: dry weight

Distance from vent (cm)	Chlorophyll *a* (µg g^{-1} DW)	Phaeopigments (µg g^{-1} DW)	Carbohydrates (mg g^{-1} DW)	Proteins (mg g^{-1} DW)	Lipids (mg g^{-1} DW)	BPC (mg g^{-1} DW)
0 (caldera)	6.15 ± 0.19	2.42 ± 0.94	0.56 ± 0.12	0.58 ± 0.08	0.03 ± 0.01	0.52 ± 0.09
10	0.23 ± 0.07	0.76 ± 0.21	0.13 ± 0.03	0.28 ± 0.04	0.06 ± 0.02	0.23 ± 0.05
100	0.70 ± 0.08	1.33 ± 0.29	0.17 ± 0.03	0.39 ± 0.05	0.07 ± 0.02	0.31 ± 0.05
200 (control)	3.76 ± 0.80	9.07 ± 0.26	0.39 ± 0.02	0.86 ± 0.00	0.24 ± 0.04	0.76 ± 0.04

Table 2. Meiofaunal density (ind. 10 cm^{-2}) at different distances from the vent, and number of higher taxa at the stations sampled

Taxa	10 cm	100 cm	200 cm
Nematodes	25.15 ± 12.25	148.63 ± 56.42	1735.58 ± 672.11
Copepods	17.97 ± 8.80	443.94 ± 136.63	1213.57 ± 486.99
Polychaetes	0.33 ± 0.57	32.99 ± 20.12	80.69 ± 58.52
Bivalves	1.63 ± 2.83	0.98 ± 0.98	3.92 ± 1.96
Ostracods	0.98 ± 1.70	0.00 ± 0.00	1.63 ± 1.50
Kinorhynchs	0.00 ± 0.00	0.00 ± 0.00	3.92 ± 3.53
Turbellarians	0.00 ± 0.00	13.07 ± 14.35	88.85 ± 16.76
Oligochaetes	0.00 ± 0.00	1.31 ± 2.26	7.51 ± 6.22
Tardigrades	0.00 ± 0.00	0.33 ± 0.57	0.33 ± 0.57
Gastrotrichs	0.33 ± 0.57	2.94 ± 5.09	2.29 ± 1.50
Cumaceans	0.00 ± 0.00	0.00 ± 0.00	3.27 ± 4.08
Amphipods	0.00 ± 0.00	0.00 ± 0.00	0.98 ± 0.98
Isopods	0.33 ± 0.57	0.00 ± 0.00	0.65 ± 1.13
Tanaidaceans	0.00 ± 0.00	0.33 ± 0.57	0.33 ± 0.57
Acarines	0.00 ± 0.00	0.65 ± 0.57	0.98 ± 1.70
Nemertines	2.61 ± 2.99	7.19 ± 6.53	72.85 ± 15.26
Priapulids	0.00 ± 0.00	0.00 ± 0.00	3.27 ± 5.66
Total abundance	49.33 ± 8.33	652.35 ± 3.44	3220.61 ± 1179.60
Number of higher taxa	8	11	17

species were found. The species *Acanthonchus* sp. 1 and *Acanthonchus* sp. 2, *Actinonema* sp. 1, *Comesoma* sp. 1, *Eurystomina ornata*, *Parachromadorita* sp. 1, *Paracyatholaimus* sp. 1, *Poligastrophora* sp. 1, *Pomponema* sp. 2, *Prochromadorella* sp. 1 and *Spiliphera.* sp. 1 were exclusively encountered at a distance of 100 cm from the vent, whereas, at a distance of 200 cm, we encountered the following exclusive species: *Acantholaimus* sp. 1, *Desmodora* sp. 1, *Doliolaimus* sp. 1, *Euchromadora* sp. 1, *Metadesmolaimus* sp. 1, *Metalinhomoeus* sp. 1, *Paradesmodora* sp. 1, *Prooncholaimus* sp. 1 and *Prooncholaimus* sp. 2, *Theristus* sp. 1 and *Wieseria* sp. 1 and *Wieseria* sp. 2 (Table 6).

The trophic structure of nematode assemblages was dominated by epistrate feeders (2A) at all stations (range: 45 to 78%). Predator-omnivores (2B) co-dominated in sediments at 10 cm from the caldera, accounting for ca. 43% of the total nematode abundance and for 39% at 100 cm (Fig. 5). The index of trophic diversity (expressed by 1 – ITD) decreased with increasing distances from the vent (Table 4; ANOVA, $p < 0.05$). The maturity index also decreased with increasing distances from the vent (Table 4; ANOVA, n.s.). The species-level *k*-dominance curves for the 10, 100 and 200 cm sites showed dominance by a single species, especially for the 200 cm site (Fig. 6A). SIMPER analysis revealed a similarity of 33% at 10 cm, a similarity of 51% at 100 cm and a similarity of 76% at a distance of 200 cm from the vent. The dissimilarity was

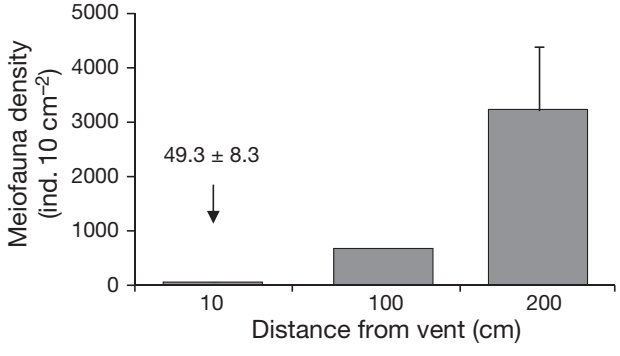

Fig. 3. Total meiofaunal density in the soft sediments at increasing distances from the vent

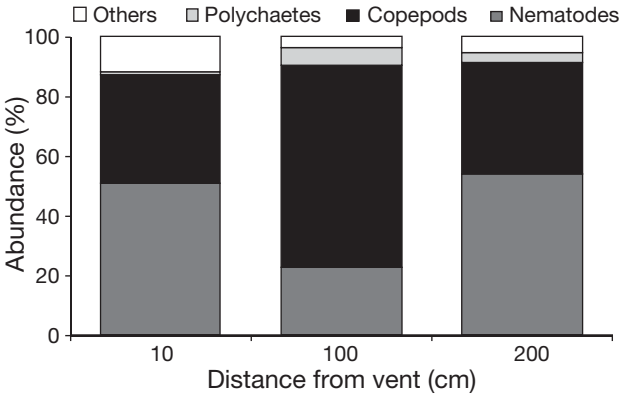

Fig. 4. Meiofaunal community structure. Reported are nematodes, copepods (copepods and their nauplii), polychaetes and other organisms. Others: bivalves, gastrotrichs, nemertines, ostracods, isopods, turbellarians, oligochaetes, tardigrades, tanaidaceans, acarines, kinorhynchs, cumaceans and amphipods

Table 3. Total and individual nematode biomass. Reported are average values ± SD (n = 100)

Distance from vent (cm)	Biomass	
	Total (µg C 10 cm^{-2})	Individual (µg C $ind.^{-1}$)
10	1.5 ± 0.8	0.06 ± 0.01
100	10.6 ± 6.2	0.07 ± 0.02
200	111.9 ± 47.2	0.06 ± 0.01

Table 4. Indices of diversity at all sampling stations—nematode species richness (SR), the indexes of Shannon-Wiener (*H'*), Margalef (*D*), Pielou (*J*) and the expected species number (ES[51]), the maturity index (MI) and the index of trophic diversity (ITD), expressed by 1 – ITD

Distance from the vent (cm)	SR	*H'*	*D*	*J*	E(51)	MI	1 – ITD
10	11	3.1	2.69	0.89	11	3.0	0.61
100	22	3.2	3.90	0.72	11.2	2.8	0.50
200	21	2.5	3.61	0.56	8.7	2.4	0.36

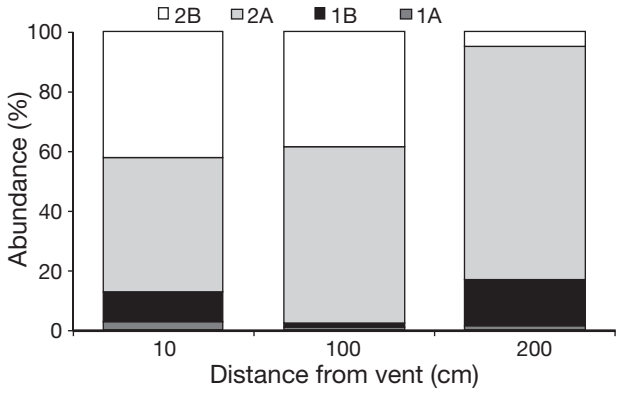

Fig. 5. Nematode trophic structure. Reported are 1A (deposit feeders), 1B (non-selective deposit feeders), 2A (epigrowth feeders) and 2B (predators) at the sampling stations at increasing distances from the vent

77% between 10 and 100 cm sites, 88% between 10 and 200 cm sites, and 78% between 100 and 200 cm sites. The analysis of similarities in species composition (ANOSIM) revealed that nematode assemblages at each station were significantly different from those at all other stations ($p < 0.05$; $R = 0.567$; number of permutations = 280; Fig. 6B). The *k*-dominance curves based on meiofaunal taxa at a distance of 10, 100 and 200 cm from the vent are reported in Fig. 7A. The MDS based on taxa revealed that each station was different from each other station (Fig. 7B). The rarefaction curves at 10, 100 and 200 cm from the vent are illustrated in Fig. 8. The expected number of species was plotted against the number of nematodes and displayed the same pattern at 100 and 200 cm from the vent, while at 10 cm from the vent the saturation value was rapidly reached.

Table 5. Nematode families (% of total abundance) at the investigated sampling sites (10, 100 and 200 cm from the hydrothermal vent)

10 cm		100 cm		200 cm	
Family	%	Family	%	Family	%
Cyatholaimidae	42.5	Cyatholaimidae	52.1	Chromadoridae	76.4
Chromadoridae	30.0	Chromadoridae	37.4	Axonolaimidae	7.5
Oncholaimidae	15.0	Oncholaimidae	7.8	Xyalidae	7.1
Axonolaimidae	5.0	Enchelidiidae	0.9	Oncholaimidae	4.7
Xyalidae	5.0	Ethmolaimidae	0.9	Desmodoridae	1.6
Linhomoeidae	2.5	Axonolaimidae	0.5	Oxystominidae	1.2
		Linhomoeidae	0.5	Cyatholaimidae	0.4
				Linhomoeidae	0.4
				Sphaerolaimidae	0.4

DISCUSSION

Effects of vent emissions on environmental and trophic variables

Deep-sea hydrothermal emissions are known to significantly alter temperature, pH and the overall chemistry of the water column around vents (Van Dover & Lutz 2004). The environmental conditions in close proximity of the shallow-water vent investigated in the present study can be

Table 6. List of nematode species encountered in the soft sediments at increasing distances (10, 100 and 200 cm) from the hydrothermal vent, and % of total abundance

10 cm		100 cm		200 cm	
Species	%	Species	%	Species	%
Pomponema sp. 1	26.8	*Pomponema* sp. 1	29.7	*Dichromadora* sp. 1	46.9
Dichromadora sp. 1	17.1	*Dichromadora* sp. 1	18.3	*Steineridora* sp. 1	24.8
Oncholaimus sp. 1	14.6	*Dichromadora* sp. 3	12.8	*Parodontophora* sp. 1	7.5
Paracanthoncus sp. 1	7.3	*Paracanthoncus* sp. 1	11.0	*Daptonema* sp. 1	6.7
Praeacanthoncus sp. 1	7.3	*Oncholaimus* sp. 1	6.8	*Dichromadora* sp. 2	2.8
Steineridora sp. 1	7.3	*Acanthonchus* sp. 1	5.5	*Oncholaimus* sp. 1	2.8
Daptonema sp. 1	4.9	*Paracyatholaimus* sp. 1	3.7	*Desmodora* sp. 1	1.2
Dichromadora sp. 3	4.9	*Spiliphera* sp. 1	2.3	*Euchromadora* sp. 1	1.2
Parodontophora sp. 1	4.9	*Steineridora* sp. 1	1.4	*Prooncholaimus* sp. 1	0.8
Terschellingia sp. 1	2.4	*Acanthonchus* sp. 2	0.9	*Viscosia glabra*	0.8
Incertae sedis	2.4	*Actinonema* sp. 1	0.9	*Wieseria* sp. 2	0.8
		Comesoma sp. 1	0.9	*Acantholaimus* sp.1	0.4
		Dichromadora sp. 2	0.9	*Dichromadora* sp. 3	0.4
		Praeacanthoncus sp. 1	0.9	*Doliolaimus* sp. 1	0.4
		Viscosia glabra	0.9	*Metadesmoliamus* sp. 1	0.4
		Eurystomina ornate	0.5	*Metalinhomoeus* sp. 1	0.4
		Parachromadorita sp. 1	0.5	*Paradesmodora* sp. 1	0.4
		Parodontophora sp. 1	0.5	*Praeacanthoncus* sp. 1	0.4
		Polygastrophora sp. 1	0.5	*Prooncholaimus* sp. 2	0.4
		Pomponema sp. 2	0.5	*Theristus* sp. 1	0.4
		Prochromadorella sp. 1	0.5	*Wieseria* sp. 1	0.4
		Terschellingia sp. 1	0.5		

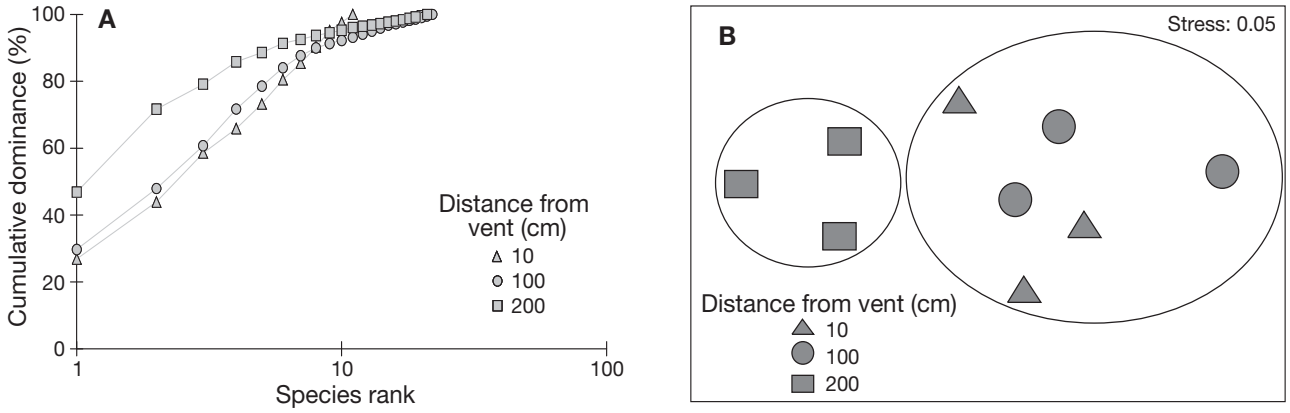

Fig. 6. *k*-dominance plots based on (A) species richness and (B) multi-dimensional scaling analysis performed using species composition. Species abundance was presence/absence transformed

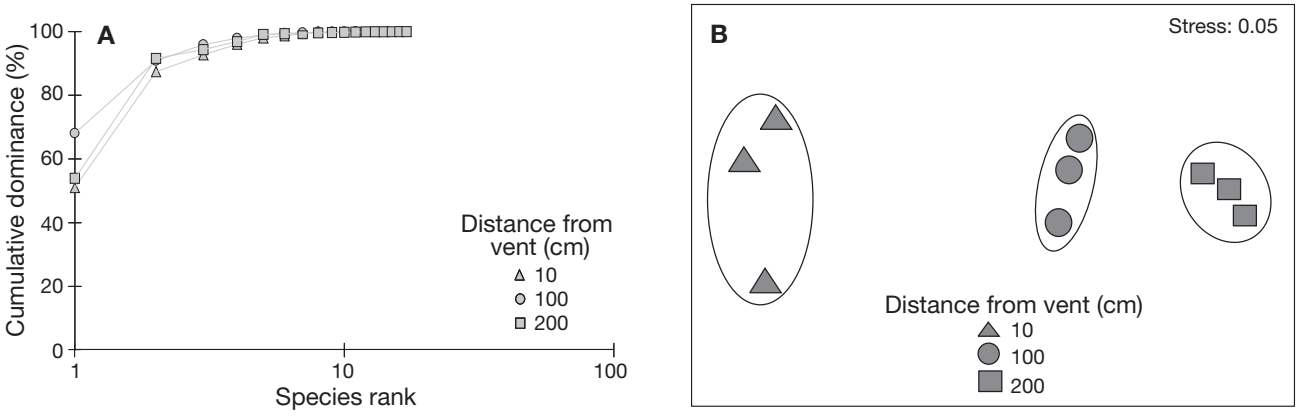

Fig. 7. *k*-dominance plots based on (A) richness of taxa and (B) multi-dimensional scaling analysis performed using taxonomic composition. Total number of taxa was square-root transformed

considered extreme. Temperatures >35°C are rarely found in marine environments, and values >70°C can seriously compromise the survival of higher life forms, especially in the case of benthic organisms that display limited mobility, such as meiofauna. Therefore, the temperatures (55 to 74°C) and pH values (<7) observed at 10 and 100 cm from the caldera were hostile for most of marine metazoans. At deep-sea vents, anoxygenic photosynthetic and sulphur bacteria are often found (Van Dover et al. 1996, Yurkov & Beatty 1998). These chemoautotrophic bacteria are known to possess bacterio-chlorophyll (Nisbet et al. 1995, Beatty et al. 2005), thus explaining the very high chl *a* concentrations reported within the compact sediments of the caldera. Chl *a* concentrations were also relatively high in the sediments surrounding the caldera. At other shallow-water vents, such as in Kraternaya Bay (Sorokin et al. 2003) and in Paleohori Bay, blooms of diatoms have been reported (Dando et al. 1995). Furthermore, Tarasov et al. (1990) and Tarasov et al. (1999) reported significantly higher concentrations of photosynthetic pigments in a vent area than at control sites. In light of the chl *a*

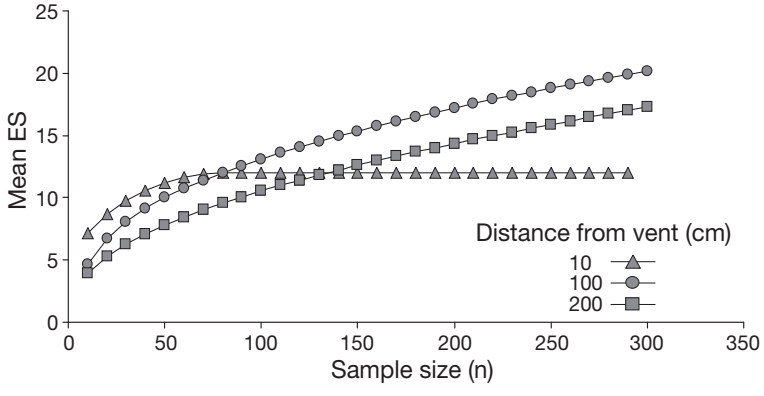

Fig. 8. Composite rarefaction curves of nematode biodiversity at increasing distances from the vent. ES: expected species number

concentrations and the ratio between active and degraded pigments (chl *a*:phaeo ratio) reported in the present study and on the basis of the extensive literature available on these variables in marine sediments (see Pusceddu et al. 2009), we hypothesize that the solid sediments of the caldera hosted a rich assemblage of chemo- and photo-autotrophic prokaryotes and that the soft sediments around the caldera hosted a large micro-phytobenthic biomass.

The sediments surrounding the shallow-water vent exhibited a relatively low organic matter concentration (<0.76 mg C g^{-1}). This value is consistent with previous data reported for other coastal sediments in the Pacific Ocean, but is higher than those observed in deep-sea sediments (A. Pusceddu et al. unpubl. data). Since the abundance and biomass of the interstitial fauna around the vent were quite low, it is reasonable to conclude that most of the biopolymeric C was due to organic detritus. The high temperatures and low pH around the vent increased the degradation rates and hydrolysis of the biopolymeric pools, thus contributing to the maintenance of low organic carbon concentrations (Svensson et al. 2004).

Effects of vents on meiofaunal biodiversity

A dramatic decrease in the abundance and diversity of organisms moving towards the vent emission was expected, due to the extreme chemical and physical conditions there. However, the abundances reported here are higher than those at other coastal vents, where meiofaunal abundances were typically 10 times lower than in the present study (Colangelo et al. 2001).

Available information on meiofauna at deep-water vents suggests the presence of obligate meiofaunal taxa (Tarasov et al. 2005). Nematodes are a key component of the meiofauna inhabiting sediments around the vents (Fricke et al. 1989, Kamenev et al. 1993, Dando et al. 1995, Thiermann et al. 1997). In the present study, nematodes dominated at 10 and 200 cm from the vent, but at a distance of 100 cm, copepods accounted for 68% of the total meiofaunal abundance. Similar results were reported by Colangelo et al. (2001) in sediments with moderate fluid emissions and by Coull (1985), which suggested that the dominance of copepods could be explained by the effect of the fluid emission that alters the sediment grain size. The presence of sulphate-reducing bacteria in close proximity to this vent (Manini et al, 2008) can provide the food needed to sustain the dominance of nematodes (Giere 1992), but the reason for the dominance of copepods at 100 cm from the vent remains unclear.

In the vent we studied, nematode species richness and the expected number of species ES(51) displayed highest values at 100 cm from the caldera. Similar results were reported for copepods by Colangelo et al. (2001) in a shallow vent in the Tyrrhenian Sea. Also biodiversity composition was significantly different among sites. Both *k*-dominance curves and the MDS plot (Fig. 6A, B) revealed that nematode species compositions at 10 and 100 cm from the vent were different from the assemblages in control sediments.

In the deep-sea hydrothermal sites of the North Fiji Basin, the genera *Leptolaimus*, *Molgolaimus* and *Monhystera* were dominant (*Molgolaimus* amounted to 63% of the nematodes; Vanreusel et al. 1997). In the meiobenthos associated with mussel aggregations from deep-sea vents, the genera *Thalassomonhystera* reached a proportion of 47% of the meiofaunal assemblage (Zekely et al. 2006). In the present study, we observed a lack of the genera that dominated deep-sea hydrothermal vents. Compared to deep-sea vents, where none of the nematode species found in hydrothermal sediments occurred in the surrounding area (Vanreusel et al. 1997), in shallow vent areas nematodes included a subset of species that lived in control sediments but were also able to survive in extreme conditions.

In proximity to the caldera, we observed the presence of nematodes belonging to the family Oncholaimidae (genus *Oncholaimus*). This was also found in Matupi Harbour and in the vents off Milos Island (Aegean Sea) (Thiermann et al. 1994, Dando et al. 1995). In particular, *Pomponema* sp. 1 (26.8%), *Dichromadora* sp. 1 (17.1%) and *Oncholaimus* sp. 1 (14.6%) were the dominant species 10 cm from the caldera. *O. campilocercoides* was found to dominate in sulphidic sediments of the shallow-water vents in the Aegean Sea (Thiermann et al. 1994, 1997), as well as in brackish waters in the Baltic and Black Seas. The genus *Oncholaimus* also tolerates extreme geothermal and hypersaline conditions and high sulphide concentrations (Gerlach & Riemann 1973, Thiermann et al. 1994), and it is a predator/omnivore/scavenger species (Teal & Wieser 1966, Jensen 1987). This species is indeed able to produce sulphur-containing droplets when exposed to hydrogen sulphide (Thiermann et al. 1994), thus reducing the concentration and toxic effect of H_2S. The accumulation of elemental sulphur also provides an energetic 'deposit' for later oxidation to thiosulphate, sulphite, or sulphate under oxic conditions (Thiermann et al. 2000).

The trophic structure of assemblages inhabiting shallow-water vents was different from that reported for deep-sea vents. At shallow depths, photosynthetic primary production is associated with chemosynthetic production, although this latter usually plays a secondary role (Tarasov et al. 2005). Therefore, the bulk of biomass does not depend on symbiotrophs, but on

organisms that feed on the available organic resources (i.e. deposit feeders, predators, omnivores, etc.). Previous studies on shallow vents provided conflicting results, in Paleohory Bay scavengers were dominant (Thiermann et al. 1997), while in Kraternaya Bay the main trophic resource was represented by diatoms, thus leading to the dominance of epistrate (diatom) feeders (Kharlamenko et al. 1995). In the present study, the nematode community was dominated by epistrate feeders, which were favoured by the high primary biomass. The lack of symbiotic organisms and the presence of the genus *Oncholaimus*, which can also feed on 'sulphur-bacteria', suggest that the microbial biomasses in shallow vents can represent an important food source capable of influencing the trophodynamics of these extreme systems.

Nematode abundances were rather low in proximity to the vent. Also, the dominance curves showed a higher dominance of fewer species at 200 cm distance from the vent, compared to low dominance close to the vent. Typically, under extreme conditions, a few 'adapted' species dominate; however, this was not the case at our study site. In proximity to the caldera we found a subset of species from adjacent areas. Since these species in proximity to the vent occurred at lower abundances than in the control sediments, it might be hypothesized that the populations close to the vent are the result of a constant colonization from adjacent areas.

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