

**Nematodes from
cold seeps**

N. Lampadariou et al.

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Influence of chemosynthetic ecosystems on nematode community structure and biomass in the deep eastern Mediterranean Sea

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Abstract

Mud volcanoes are a special type of cold seeps where life is based on chemoautotrophic processes. They are considered as extreme environments and are characterised by unique megafaunal and macrofaunal communities. However, very few studies on mud volcanoes taking into account the smaller meiobenthic communities have been carried out. Two mud volcanoes were explored during the MEDECO cruise (2007) with the Remotely Operated Vehicle (ROV) Victor-6000; Amsterdam, located south of Turkey between 1700 and 2000 m depth (Anaximander mud field) and Napoli, south of Crete, located along the Mediterranean Ridge at about 2000 m depth (Olimpi mud field). The major aim of this study was to describe distributional patterns of meiofaunal communities and nematode assemblages from different seep microhabitats. Meiofaunal taxa and nematode assemblages at both mud volcanoes differed significantly from other Mediterranean sites in terms of standing stocks, dominance and species diversity. Density and biomass values were significantly higher at the seep sites, particularly at Amsterdam. Nematodes, the dominant meiofaunal taxon, displayed deeper penetration vertically into the sediment at the seep areas, indicating that biological rather than physicochemical factors are responsible for their vertical distribution. Patterns of nematode diversity varied, displaying both very high or very low species richness and dominance, depending on the habitat studied. The *Lamellibrachia* periphery and mussel bed of Napoli exhibited the highest species richness while the reduced sediments of Amsterdam yielded a species-poor nematode community, dominated by two successful species; one belonging to the genus *Aponema* and the other to the genus *Sabatieria*. Analysis of β -diversity showed that habitat heterogeneity of mud volcanoes contributed substantially to the total nematode species richness in the eastern Mediterranean Sea. These observations indicate a strong influence of mud volcanoes and cold-seep ecosystems on the meiofaunal communities and nematode assemblages.

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1 Introduction

Cold seeps, which have been known for over 30 yr (Paull et al., 1984; Suess et al., 1985), are characterized as extreme environments occurring in a wide variety of geological settings along both active and passive margins (Sibuet and Olu, 1998; Levin, 2005). They are commonly found in the Pacific, Atlantic and Indian Oceans and are known to host highly diverse and abundant chemosynthetically-based communities (Carney, 1994). More recently, seep communities have been also reported in the Mediterranean Sea (Corselli and Basso, 1996).

Submarine mud volcanoes are a special type of cold seep where over-pressurized sediment leaks from deeper layers in the form of mud and fluid through the sea floor (Milkov, 2000; Dimitrov, 2002). These are often accompanied by large quantities of gas emissions, such as methane, commonly originating from deep, subsurface sedimentary layers located several kilometers deep (Milkov, 2000; Kopf, 2002). These gas emissions are taken up by archaea and bacteria through chemoautotrophic processes to produce sulfides, which may be further utilized by symbiotic bacteria to sustain high biomass production in invertebrates (Olu-Le Roy et al., 2004; Fiala-Médioni and Felbeck, 1990; Fisher, 1990). The study of submarine mud volcanoes has attracted a lot of attention over the last decades since it may provide useful insights into early meta-zoan life. Deep-sea hypoxic environmental conditions are believed to resemble the late Archaean or Proterozoic Eons, when oxygen levels were similarly low and the origin and initial diversification of Eucarya has occurred.

Most biological studies of cold seeps and submarine mud volcanoes have focused on large, symbiont-bearing megafauna, such as siboglinid tube worms, mytilid mussels and vesicomid clams (Levin and Mendoza, 2007; Sibuet and Olu, 1998; Kojima, 2002; Sibuet and Olu-LeRoy, 2002; Tunnicliffe et al., 2003), or on microbiological processes (Valentine and Reeburgh, 2000; Hinrichs and Boetius, 2002; Valentine, 2002). Several studies have also examined the smaller infaunal communities (predominantly macro-fauna), suggesting that their densities may be higher or similar compared to non-seep

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communities (Menot et al., 2010; Levin and Mendoza, 2007; Levin et al., 2000; Davis and Spies, 1980; Levin et al., 2003). Recently, such studies have also included the eastern Mediterranean (Ritt et al., 2011, 2012). On the other hand, meiofauna studies from seep areas, particularly mud volcanoes, are generally scarce and until the very recent studies of Zeppilli et al. (2011a, 2012) completely absent from the Mediterranean. Previous studies, mainly from the Arctic, the Gulf of Mexico, Barbados and the Japan Trench have reported that, similar to macrofauna, there is no unequivocal response of the metazoan meiofauna to the different seep conditions (Olu et al., 1997; Shirayama and Ohta, 1990; Buck and Barry, 1998; Levin, 2005). The increased habitat heterogeneity found in cold-seep areas often results in an unpredictable high variability of meiofaunal densities within the seeps, relative to the surrounding sediment (Montagna and Spies, 1985; Levin, 2005; Cordes et al., 2010; Ritt et al., 2012). In regard to nematode diversity, which is generally the dominant taxon, the results were inconsistent, with some studies showing an exceptionally high dominance of only one species (Van Gaever et al., 2006) while others reported a species-rich community with many overlapping families or genera between seep and nearby control sediments (Shirayama and Ohta, 1990; Pape et al., 2011). Nevertheless, in most of these studies, dominance was usually higher and species diversity was lower when compared to surrounding pristine areas (Van Gaever et al., 2006, 2010; Shirayama and Ohta, 1990).

The present study provides a detailed quantitative analysis of the meiofauna communities from two different mud volcanoes in the eastern Mediterranean: Amsterdam and Napoli. They were the target of an interdisciplinary cruise (MEDECO, 2007), which one of the main objective was to investigate the microbial as well as the meio-, macro- and megafaunal communities from several reduced deep-water environments including mud volcanoes, brine seeps and pockmark areas along the Mediterranean Sea. Previously, Ritt et al. (2012), described the structure of macrofaunal communities (> 250 μm) in relation to the environmental conditions of the two mud volcanoes. Regarding the meiofauna, the main objective of the cruise was to quantify the communities from different microhabitats in terms of species diversity, abundance and biomass; with

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a special focus on nematodes, the most abundant group. The various microhabitats were chosen on the basis of differences in sediment chemistry and appearance as evidenced both from observations with the ROV Victor-6000 as well as from previous observations during the MEDINAUT cruise in 1998.

5 More specifically, the following questions were addressed:

1. Are meiofaunal standing stocks as well as local (alpha) diversity enhanced in mud volcanoes compared to nearby deep-sea sediments?
2. Do mud volcanoes harbour faunal assemblages distinct from adjacent deep-sea sediments, thus enhancing regional (gamma) biodiversity?
- 10 3. How do the meiofaunal assemblages vary among mud volcanoes at a regional scale?
4. Do different mud volcanoes harbour a distinct and specialized fauna?

2 Materials and methods

2.1 Study areas and habitats

15 Sediment samples were collected during Leg 1.3 of the MEDECO cruise (MEditerranean Deep-sea ECOsystems) aboard the French R/V *Pourquoi Pas?*, which was equipped with the Remotely Operated Vehicle (ROV) Victor-6000. This leg of the cruise took place between 18 and 31 October, 2007. In total, ten different microhabitats were sampled; five from the Amsterdam and four from the Napoli mud volcano. In addition,
20 one control sample was collected from an area outside the influence of the mud volcanoes. The five habitats from the Amsterdam mud volcano were: (i) *Lamellibrachia* field; (ii) *Lamellibrachia* periphery; (iii) mussel bed; (iv) the summit of the mud volcano; and (v) a gas emission area, hereafter referred to as the reduced sediment area. The four microhabitats from the Napoli mud volcano were: (i) *Lamellibrachia* field; (ii)

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Lamellibrachia periphery; (iii) mussel bed; and (iv) mussel bed periphery. A detailed description of the two areas and habitats as well as of the sampling methodology follows.

2.1.1 Amsterdam mud volcano

Amsterdam is an elliptical seafloor feature, up to 3 km wide and 100 m high, located in the area southwest of Turkey (Fig. 1). It has a very rough morphology with depressions and abrupt scarps, particularly on its summit (2040 m depth) due to an erupted mud flow over 300 m thick. The substratum is characterized by the presence of carbonate crusts, muddy areas and rock clasts (i.e. rock fragments that come from deeper layers and are expelled on the seafloor with fluid/gas emissions). Temperature measurements in the centre of this mud volcano support the presence of a high seepage activity, with a temperature reaching 36 °C, 7 m deep within the sediments (Foucher unpublished data, MEDECO 2007). No brine pools were ever observed on Amsterdam (Zitter et al., 2005). Bivalve shells and tubeworms were seen close or under carbonate crusts.

The *Lamellibrachia* area consisted of black sediments, where dense bush-like clusters of the tube worm *Lamellibrachia anaximandri* occurred. Samples were obtained from: (i) patches of brown normal-looking sediment found in the immediate vicinity (less than 1 m distance) of the tube worms, hereafter referred to as the *Lamellibrachia* field; and (ii) from a distance of approximately 7–10 m from the tube worms, hereafter referred to as the *Lamellibrachia* periphery. The mussel bed microhabitat on the other hand, consisted of soft sediments covered by large numbers of small bivalves from 2 families (*Mytilidae* and *Vesicomysidae*). In some cases, this habitat was characterized by large pieces of carbonate crust covered with dead mussels belonging to the genus *Idas* instead. Infrequent live specimens of *Lamellibrachia* were visible as well. The reduced sediment was an interesting active site where gentle gas emissions were observed. The summit of the mud volcano was also sampled, however it was completely covered with large amounts of clasts of various types (both small and large) and therefore

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sampling was only possible by means of the box corer. Two pseudo-replicates were obtained from this area by subsampling one box core deployment. A summary of station parameters, habitat type and number of samples obtained from Amsterdam mud volcano is provided in Table 1.

5 A control station, located approx. 2 nm to the northeast of Amsterdam and completely outside the influence of the mud volcano, was also sampled (Fig. 1). Only one control sample could be obtained from one multiple corer deployment.

2.1.2 Napoli mud volcano

10 Napoli is a dome-shaped feature, 1000 m wide and 200 m high, located south of Crete. It is located at 1950 m depth and is commonly surrounded by irregular mud flows and circular depressions. Fresh mud flows and brine pools were observed on the summit, indicating intense degassing (Charlou et al., 2003). Brines are formed by salt-bearing sediments dissolved by warm fluids. Therefore, brine seepage to the seafloor is a result of fluid release along faults piercing the evaporites. The muddy brines are often rich in thermogenic and biogenic hydrocarbon gases produced below the evaporites. On this mud volcano, benthic communities (e.g. tubeworms, bivalves) were observed at the periphery of the centre, avoiding the proximity of brines where the salinity can reach up to 83 g L^{-1} salt (Charlou et al., 2003). During the MEDECO cruise (2007), many empty brines and “dried” brine rivers were surveyed on the flanks which were considered as fossil brines. The brine pools reported during previous cruises (MEDIN-AUT 2000, NAUTINIL 2003) were not re-observed during MEDECO, suggesting that fluid/gas emissions are variable in time and space.

25 Regarding the four habitats sampled from Napoli, the *Lamellibrachia* area was characterized by black sediments where dense, bush-like clusters of the tube worm *Lamellibrachia anaximandri* occurred. Samples were again obtained from two different areas: (i) from patches of brown, normal-looking sediment found in the immediate vicinity (less than 1 m distance) of the tube worms, hereafter referred to as the *Lamellibrachia* field; and (ii) from a distance of approximately 7 m from the tube worms, hereafter referred

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to as the *Lamellibrachia* periphery. Similarly, the mussel bed area consisted of large numbers of dead bivalve shells belonging mainly to the family Lucinidae. Again, two areas were sampled: (i) at a distance of less than 1 m from the bivalve shells, hereafter referred to as the mussel bed; and (ii) at a distance of approximately 7 m from the shells, hereafter referred to as the mussel bed periphery. Table 1 provides a summary of station parameters, habitat type and number of samples obtained from the Napoli mud volcano.

2.2 Sampling and sample processing

Most samples were collected by means of the video-guided ROV Victor-6000; the exceptions being the summit and the control area of the Amsterdam mud volcano, which were sampled by means of a USNEL box corer and a multiple corer, respectively. All samples were collected with clear plastic tube corers of 5.4 cm inner diameter to a depth of 10 cm. In the case of the box or multiple corer sampling, sub-sampling was performed (\varnothing 5.4 cm). As soon as the cores were retrieved, the overlying water was filtered through a 32 μ m mesh size sieve and the material retained on the sieve was backwashed into the plastic containers where samples were stored for later laboratory analysis. All sediment cores were then cut into 1 cm thick horizontal slices to a depth of 5 cm. Prior to fixation with 4 % buffered formalin, samples were placed in a 6 % MgCl₂ solution for approximately 15 min to promote tissue relaxation. Metazoan meiofaunal organisms were extracted from the residue by floatation with Ludox (1.15 specific gravity) and stained with Rose Bengal. Organisms were sorted and identified to major taxonomic level under a stereoscopic microscope. At least 100 nematodes from the top sediment section and, depending on their relative abundance, 10 to 60 nematodes from each of the remaining sections were randomly picked out, mounted on glycerine slides and identified to species level. Nematode classification was based on the pictorial keys of Platt and Warwick (1983, 1988) and Warwick et al. (1998) as well as relevant literature dealing with genera and species from the Mediterranean Sea. The same specimens used for identifications were also used for the determination of

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nematode biomass. Nematode wet weight (WW) was calculated following Andrassy's formula: Biomass ($\mu\text{g WW}$) = $L \times W^2 / 1\,600\,000$; where L is nematode length and W is nematode width (Andrassy, 1956). Dry weight (DW) was assumed to be 25 % of WW (Wieser, 1960). All values reported here are in $\mu\text{g DW}$, length and width are expressed in μm .

2.3 Data analysis

Differences in faunal parameters were assessed by one-way or two-way analyses of variance (ANOVA), followed by pairwise comparisons based on the Tukey Honestly Significant Difference test (Tukey HSD). When necessary, data were first $\log(x + 1)$ transformed and Bartlett's test was used to check the assumption of homoscedasticity.

Nematode diversity was calculated and expressed as Hill numbers of the orders N_0 , N_1 , N_2 and N_∞ (Hill, 1973), as recommended by Heip et al. (1988). These indices differ in their tendency to give different weight to the less common species. The impact of dominance increases and the influence of species richness decreases with increasing order of the diversity number. In addition, two levels of differentiation diversity were measured using the Marczewski–Steinhaus distance (C_{MS}), which is the complement of the Jaccard similarity index: (1) beta diversity, the change of diversity within and between habitats for each mud volcano, and (2) delta diversity, the change of diversity between mud volcanoes.

All analyses and graphs were performed using R (R Core Team, 2012) with the exception of differentiation diversity measures and the nMDS graph for which Primer v. 6.1.3 (Clarke and Gorley, 2006) was used.

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3 Results

3.1 Standing stocks

An overview of the meiofaunal taxa composition and densities for the different habitats of the Amsterdam and Napoli mud volcanoes as well as for the control sample is given in Table 2. Altogether, 23 metazoan meiofaunal groups were found, with the highest number being recorded at the summit of Amsterdam (15 taxa) and the lowest at the *Lamellibrachia* field of Napoli (8 taxa) and the control station (9 taxa). Taxa that were not encountered at the control station but were regularly found in other habitats included kinorhynchs, cumaceans, gastrotrichs, halacaroids and some temporary meiofauna such as bivalves, gastropods and amphipods. The same taxa were also missing from the *Lamellibrachia* field of Napoli but generally, there was no common pattern of how the rare taxa were distributed among the habitats.

Meiofauna was generally dominated by nematodes, which ranged from 82.4 to 95.7%. They were followed by harpacticoid copepods which, together with their nauplii, ranged from 2.6 to 10.8%. Other taxa with significant contributions were annelids (including Polychaeta, Oligochaeta and Annelida "Incertae sedis"), ranging from 0.8 to 2.3%, and molluscs ranging from 0.1 to 2.9%. All other taxa, including both permanent and temporal meiofauna, contributed less than 1% (Table 2). The highest meiofauna densities (Fig. 2) were recorded at the mussel bed habitat of Amsterdam (1992 ind./10 cm²) and the lowest at the control station (119 ind./10 cm²). Average densities for Amsterdam and Napoli were 1281 ± 519 and 586 ± 329 ind./10 cm², respectively. Nematode densities followed the same pattern, with the highest values occurring at the mussel bed of Amsterdam (1835 ind./10 cm²) and the lowest at the control station (108 ind./10 cm²). Average values were 1152 ± 528 and 535 ± 295 ind./10 cm² for Amsterdam and Napoli, respectively (Fig. 3). Two-way ANOVA with "Area" and "Habitat type" as main factors showed a significant "Area" effect for both meiofaunal and nematode densities, with Amsterdam differing from the control station in both cases (Tukey

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HSD: $P < 0.05$), while it further differed from Napoli for meiofauna (Tukey HSD: $P < 0.01$).

Most meiofauna was found on the top layer of the sediment (0–1 cm) and the same pattern was also followed by nematodes, the dominant group (Fig. 4). The only exception from the above pattern occurred at the summit of the Amsterdam mud volcano where a subsurface peak (1–2 cm) was found (Fig. 4); without, however, this difference being statistically significant (Tukey HSD: $P = 0.91$).

3.2 Nematode communities

In total, more than 4000 nematodes were identified, belonging to 27 families, 83 genera and 143 species. The genera that contributed, on average, with more than 1 % to the total abundance, are listed in Table 3. From the total number of species identified, only two of them, belonging to the genus *Aponema* and *Leptolaimus*, were present at all habitats whereas 29 species (20.3 %) or 14 genera (16.9 %) were present at only one habitat. Among the two most abundant genera, *Aponema* was represented by a single species (average relative abundance: 14.0 %) while the genus *Sabatieria* was represented by a complex of three species. However, only two of them, belonging to the Pulchra group and to the Celtica group, were found in relatively high numbers (on average 13.6 % and 6.8 %, respectively). Out of the 143 species, 18 were singletons (12.6 %) and 14 were doubletons (9.8 %). *Aponema sp. 1* and *Sabatieria sp. 4*, were the most abundant species comprising, on average, 14.0 % and 13.6 %, respectively. At some habitats, they strongly dominated the community. For example, at the reduced sediment of Amsterdam, they accounted for 91.8 % of the community (*Aponema sp. 1*: 51.2 %; *Sabatieria sp. 4*: 40.6 %). Similarly, *Sabatieria sp. 4* dominated the community at the *Lamellibrachia* field of Napoli with 49.6 %. Surprisingly, *Aponema* (e.g. *Aponema sp. 1*) was also the most abundant genus at the control station (Table 3, 12.9 %) while *Thalassomonhystera*, *Manganonema* and *Acantholaimus* were ranked 2nd to 4th with 11.9 %, 6.2 % and 5.2 %, respectively (Table 3).

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When comparing the genus composition between the two mud volcanoes, they both exhibited the same pattern of dominance with *Sabatieria*, *Aponema* and *Metalinhomoeus* being the three most abundant genera comprising together 51.4 % and 33.5 % of the abundance for Amsterdam and Napoli, respectively. However, when they were compared in terms of species composition, they showed obvious differences. For example, in Amsterdam, the four most abundant species were *Aponema sp.1* (19.5%), *Sabatieria sp.1* (12.9%), *Sabatieria sp.4* (11.8%) and *Metalinhomoeus sp.1* (5.5%). On the other hand, Napoli was dominated by *Sabatieria sp.4* (19.3%), *Aponema sp.1* (7.5%), *Molgolaimus sp.1* (4.4%) and *Marylynnia sp.1* (4.3%). This pattern was confirmed by the nMDS analysis based on species composition (Fig. 5), which showed a clear separation between the Amsterdam and Napoli mud volcanoes (ANOSIM: $R = 0.47$; $P = 0.016$).

3.3 Diversity patterns

The highest number of species ($N_0 = 66$) was recorded in a sample collected from the *Lamellibrachia* periphery of Napoli and the lowest in a sample collected from the reduced sediments of Amsterdam ($N_0 = 12$). In general, species richness (Table 4) was highest at the *Lamellibrachia* periphery and mussel bed of Napoli and lowest at the reduced sediment of Amsterdam and *Lamellibrachia* field of Napoli. The control station displayed equally high species richness as the two high diversity habitats of Napoli (*Lamellibrachia* periphery and mussel bed). This pattern was retained for Hill's higher order numbers though the control station showed always higher values (Table 4). Beta diversity (Table 5) indicated that there was a high within-habitat dissimilarity, i.e. between replicates of the same habitat. Highest dissimilarity was found between the reduced sediments of Amsterdam and the rest of the studied habitats (> 0.83). Overall, differences between habitats were high (Table 5), with the exception of the pairwise comparisons between the *Lamellibrachia* periphery habitat and the two mussel bed habitats at Napoli, for which dissimilarity was below 0.50. The same trend was

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observed when comparing similar habitats between the two mud volcanoes (Table 5: δ -diversity) as differences were also high (0.58–0.74).

3.4 Morphometrics and biomass

The analysis of morphometric data showed that, on average, nematodes from cold-seep areas were much larger compared to those from the control station (Table 6). For example, the average nematode dry weight for Amsterdam, Napoli and control was 0.17, 1.83 and 0.03 μg , respectively. This large difference was due to two factors: a shift in the size spectra of seep nematodes towards longer and wider animals (Fig. 6: length and width panels) and the occurrence of a relatively high number of large nematodes at Napoli with a length $> 4000 \mu\text{m}$ (Fig. 6); whereas the largest nematode at the control station had a length of only 2782 μm . This shift in the nematode size spectra, in conjunction with the density differences found between Amsterdam, Napoli and the control station, resulted in very large biomass differences. Thus, the average total biomass at each site was 202.29, 1228.73 and 3.13 μg per 10 cm^2 for Amsterdam, Napoli and the control station, respectively.

4 Discussion

4.1 Mud volcanoes in the eastern Mediterranean

The two mud volcanoes, although very different in shape and size, share a very similar external morphology with a central mound and a moat surrounding it. This structure is commonly found in many other mud volcanoes along the European active and passive margins (e.g. Lykousis et al., 2009, and references therein) and is probably among the most common features in the Mediterranean Ridge Mud Diapiric Belt (Dimitrov, 2002). Its formation was probably caused by a collapse of the sea floor after the eruption of mud from a depth of 1 to 2 km below the mud volcano, indicating that subsidence and tectonics play an important role in the formation of these depressions (Zitter

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et al., 2005). Apart from their external morphology, the two mud volcanoes appear also to share similar microhabitats, mainly areas with the siboglinid polychaete *Lamelibrachia anaximandri*, the lucinid *Lucinoma kazani* and the mytilid *Idas modiolaeformis* (Olu-Le Roy et al., 2004; Ritt et al., 2012). However, despite their visual similarities, these habitats have inherent differences in terms of sediment chemistry and macrofaunal composition (Ritt et al., 2012). Amsterdam is characterised by the presence of gas hydrates (Lykousis et al., 2009), while Napoli is characterised by the presence of brines (Charlou et al., 2003). In addition, Amsterdam appears as more active, based on the higher sediment temperature (J. P. Foucher, personal communication, 2012) and methane concentration (Charlou et al., 2003). These differences are reflected in the distribution of macrofaunal communities, with Napoli having an overall higher taxonomic diversity and the reduced sediments of Amsterdam being mainly colonised by symbiont-bearing vesicomyid bivalves and heterotrophic dorvilleid polychaetes (Ritt et al., 2012).

4.2 Meiobenthos from seep and non-seep areas

Data from the control station of the present study are in line with previous research in the area, indicating that meiofaunal densities and biomass at bathyal and abyssal sediments of the Eastern Mediterranean are among the lowest worldwide (Lampadariou et al., 2009; Tselepides and Lampadariou, 2004; Gambi et al., 2010). This pattern has been mainly related to the highly oligotrophic conditions of the Eastern Mediterranean and a depletion of food with increasing water depth (Tselepides et al., 2004; Lampadariou and Tselepides, 2006; Danovaro et al., 2000). In contrast, the seep conditions appear to favour meiofaunal communities since both mud volcanoes showed significantly higher standing stocks when compared with the control station. The favourable seep conditions were also confirmed by the vertical distribution of nematodes, which clearly showed that there was a deeper penetration of animals into the sediment at the two mud volcanoes. Additionally, and contrary to the control station, individuals

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were regularly found even below 5 cm sediment depth (V. Kalogeropoulou, personal observation), a pattern that was also followed by most other meiofaunal taxa as well.

The comparison of meiofauna densities between the two mud volcanoes showed that meiofauna densities were significantly higher at Amsterdam. A similar pattern was also found by Olu-Le Roy et al. (2004), who compared chemosynthetic macrofaunal communities from six mud volcanoes in the eastern Mediterranean, including Amsterdam and Napoli. In their study, Olu-Le Roy et al. (2004) also reported that Amsterdam had higher values compared to Napoli, a pattern which they attributed to the higher methane fluxes in the former and the greater instability due to the existence of brine areas in the latter. Higher macrofaunal densities were also observed at Amsterdam by Ritt et al. (2012) reaching over 2.3 times that of Napoli. In contrast to the above trends for densities, the trend for biomass was opposite. This time, Napoli displayed increased values which, in fact, were one and two orders of magnitude larger compared to the control station and Amsterdam, respectively. The main reason behind these differences was an apparent shift in nematode size-spectra towards longer and wider animals at Napoli. A similar shift in nematode size spectra has been found by Vanreusel et al. (1997) at the North Fiji Basin, an adaptation that may be advantageous in thiobiotic conditions, as suggested by Jensen (1987).

The nematode community composition and richness varied strongly between habitats, displaying some notable features. The community at the reduced sediments of Amsterdam was dominated by two equally abundant species (*Aponema sp.1* and *Sabatieria sp.4*), which together comprised more than 90%. Similarly, the community at the Napoli *Lamellibrachia* field was dominated by only one species (*Sabatieria sp.4*), which comprised almost 50%. As a consequence of their increased dominance, these two habitats displayed very low species richness (e.g. $N_0 = 12$ and 15 for the reduced sediments of Amsterdam and the *Lamellibrachia* field of Napoli, respectively). The dominance of the genus *Sabatieria* is not surprising since it is a typical genus of suboxic or anoxic shallow-water muddy sediments, observed to thrive also in reduced deep-sea habitats such as the Storegga Siboglinidae habitat in the north Atlantic

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(Van Gaever et al., 2009b), the Darwin mud volcano seep site in the central Atlantic (Pape et al., 2011) or in the REGAB cold seep of the Gulf of Guinea in the south Atlantic (Van Gaever et al., 2009a).

Surprising however, are the high numbers of *Aponema sp. 1*, which was dominant not only at the reduced habitats of Amsterdam but also at the control station; although with a much lower percentage (12.9 % vs. 25–50 %). Another striking feature of the control station was the fact that the genus *Manganonema*, a genus that is found only rarely and in very low numbers (Zeppilli et al., 2011b), was ranked second. The above results are unexpected since in the Mediterranean, *Thalassomonhystera*, *Acantholaimus* and *Halalaimus* are usually the dominant genera at bathyal and abyssal depths (Vanreusel et al., 2010); although occasionally other genera such as *Syringolaimus*, *Sphaeoro-*
laimus and *Theristus* may also gain in importance (Vanreusel et al., 2010; Lampadariou and Tselepides, 2006; Soetaert and Heip, 1995). The dominance of *Aponema* and *Manganonema* at the control station indicates that, despite being 2 nm away from the mud volcano, this area might still be under its influence, or at least has been in the past, thus providing favourable conditions for opportunistic and tolerant species. High numbers of *Aponema* have been previously reported from the Siboglinidae fields of the Håkon Mosby Mud Volcano, although with a much lower relative abundance (12–17 %) (Portnova, 2009; Van Gaever et al., 2009b). Apart from these studies, *Aponema* is usually reported with low numbers, or, at best, as subdominant to other genera (e.g. Zeppilli et al., 2011a; Lamshead et al., 2003). Another interesting case is that of *Molgolaimus*, a genus that was ranked 2nd at the *Lamellibrachia* periphery of Napoli (8.1 %) and subdominant at the *Lamellibrachia* field of Amsterdam (6.5 %). *Molgolaimus* differs from *Aponema* in having reflexed instead of outstretched ovaries, a feature that led Lorenzen (1994), in the most recent classification of free-living nematodes, to place it in the family Desmodoridae, while previously they were both members of the same family (i.e. Molgolaimidae: Jensen, 1978). Apart from this small phylogenetic difference, the two genera are so similar in all other characteristics that we may assume that they also share similar physiological and ecological features such as tolerance to chemical

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stress, metabolism and ability to move or migrate (Peters, 1983; Soetaert et al., 2002). *Molgolaimus* has been often observed to be abundant in reduced conditions, supporting the hypothesis that it is an opportunistic genus capable of exploiting abnormal and extreme environments such as mud volcanoes, hydrothermal vents and cold seeps (Van Gaever et al., 2004; Vanreusel et al., 1997). The dominance of *Aponema* at the reduced sediments of Amsterdam clearly suggests that it is also a tolerant and opportunistic genus and that its similarities with *Molgolaimus* are not limited only to the external morphology.

The high abundance of *Manganonema* at the control station is also surprising. This genus, although present in many oceans of the world (e.g. Vanhove et al., 1999; Netto et al., 2005; Danovaro et al., 2008), is considered a rare deep-sea genus as it never exceeds 2 to 3% (Fonseca et al., 2006; Zeppilli et al., 2011b). So far, it has been reported at hydrothermal vents, mud volcanoes, submarine canyons, polymetallic nodule deposits, cold-water corals and seamounts (e.g. Zeppilli et al., 2011b, and references therein), suggesting that this genus is able to colonize many different environments. This is further supported by the present study since *Manganonema* was not only found at the control station but also at the mussel bed and *Lamellibrachia* field of Napoli as well as at the summit of Amsterdam. The high relative abundance of *Manganonema* found at the control station (6.2%) suggests that this genus might not be as rare as previously thought and that there might be specific, yet unexplored habitats, where it thrives in high numbers.

Various authors have suggested that the penetration of meiofauna into deep-sea sediments is governed directly and primarily by the oxygenation of the sediment column (Shirayama, 1984; Alve and Bernhard, 1995), while others attributed more importance to food availability (Thiel, 1983; Vanreusel et al., 1995; Lamshead et al., 1995). Under seep conditions, the macrofaunal activity (e.g. root penetrations, burrowing) may provide islands of oxygen even deeper into the sediment and thus are expected to influence the vertical distribution of microbial and smaller infaunal communities (Levin, 2005). Indeed, a deeper vertical penetration of meiofauna has been

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reported in a number of seep sites such as the Sagami Bay in central Japan, (Shirayama and Ohta, 1990), the western Mediterranean (Zeppilli et al., 2012) and the eastern Antarctic Peninsula (Hauquier et al., 2011). In the present study, nematodes penetrated deeper not only at the *Lamellibrachia* field and periphery, where root penetration might have provided corridors of O₂ transport into the sediment, but at all other seep habitats as well. Moreover, there was a subsurface peak at the summit of the Amsterdam mud volcano. This suggests that oxygen penetration or sulphide concentrations are not the main factors governing the depth penetration of meiofauna at seeps and that other factors such as food availability (e.g. high microbial concentration), sediment mixing (physical and biological) and root penetration might be equally important.

4.3 Influence of seep heterogeneity on diversity

The total number of meiofaunal taxa encountered in the present study (23 taxa) is relatively high when compared to other Mediterranean or worldwide studies (e.g. Gambi et al., 2010, and references therein); however, if one considers the different habitats separately, then the numbers (9 to 15 taxa) are within the ranges reported previously. For example, in surveys focusing specifically on cold seep areas, Van Gaever et al. (2009b) reported 13 taxa at the Siboglinidae field of the Nyegga area in the North Sea while Zeppilli et al. (2011a) reported 15 taxa at terrace-like carbonate structures in the central Mediterranean. Similarly, Zeppilli et al. (2012) found 3 to 8 taxa in a western Mediterranean pockmark area. In the present study, nematodes were by far the dominant taxon at all habitats investigated. This is usually the case in most chemoautotrophic environments, although other taxa such as gnathostomulids or copepods have been also reported to prevail (Powell and Bright, 1981; Powell et al., 1983). Nevertheless, these exceptions are usually found in shallow areas while the bulk of evidence, including the present study, indicates that in the deep-sea, cold-seep areas, particularly mud volcanoes, are always dominated by nematodes (e.g. Levin, 2005, and references therein). This is not surprising since nematodes are typically the dominant taxon in ambient deep-sea sediments (Lamshead and Boucher, 2003; Giere, 2009).

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The comparison of diversity measures of the different habitats revealed that, similar to the abundance patterns, there is no consistent response of nematode diversity to the varying seep conditions. Napoli generally displayed higher diversity values compared to Amsterdam. However, one of its habitats (*Lamellibrachia* field) had a very low number of species, similar to the most species-poor habitat, namely the reduced sediments of Amsterdam. On the other hand, the number of species encountered at the control station was equally as high as the two most diverse habitats of Napoli. It should be mentioned here that the data analysed are rather unbalanced in terms of the uneven sampling effort within habitats and between the three regions (i.e. low number of replicates for some habitats; only one sample for the control station). These kind of problems are often unavoidable in mensurative experiments (Underwood, 1996) and are very common in deep-sea surveys, particularly when advanced but expensive submersible technologies, such as ROV's, are involved. Nevertheless, the comparison of the control station in the present study with ambient sediments collected from different sites of the Mediterranean revealed no real differences in nematode species richness whatsoever (Danovaro et al., 2008). In a comparison of nematode communities from different shallow mud volcanoes in the central Mediterranean, Zeppilli et al. (2011a) found that gas seepage had a negative effect on both meiofaunal abundance and the number of higher taxa, whereas seep conditions were beneficial for nematode diversity. Similarly, in a comprehensive review of a global nematode data set, Vanreusel et al. (2010) reported that certain seep habitats, such as the well-oxygenated sediments underneath siboglinid tubeworm patches, were inhabited by a genus-rich nematode assemblage composed of genera similar to those of the slope sediments.

According to Whittaker (1972), β -diversity is defined as variation in the identities of species among different habitats or sites along transects and provides a direct link between biodiversity at local scale (α -diversity) and the broader regional species pool (γ -diversity). Thus, it is an important component of community ecology for understanding diversity patterns, i.e. change in community composition/structure along spatial and environmental gradients (Anderson et al., 2011; Ellingsen and Gray, 2002). However,

until recently, β -diversity has been widely neglected in the marine environment, particularly in meiobenthic studies (Sevastou et al., 2011). In the present study, β -diversity analysis showed that the reduced sediments of Amsterdam, with a strong dominance of two species, differed the most from all other habitats. It also showed that the highest species turnover rate occurred either between different habitats of the same mud volcano or between similar habitats of different mud volcanoes. Jumars (1976) first introduced the problem of scale in deep-sea ecology with subsequent studies, clearly indicating that diversity measures are indeed scale dependent for a wide range of organisms and habitats. In a study on the influence of cold-seep habitat heterogeneity at different spatial scales along the Norwegian margin, Van Gaever et al. (2010) showed that the macro-scale (e.g. 10 s to 100 s ms) contributed the most to nematode genus diversity. This result is very similar to the results from the present study as the within habitat, between habitat and between mud volcano complementarity analyses, roughly correspond to the micro-, macro- and mega-scales from the Norwegian margin. Nevertheless, in both of these studies, besides the higher genus or species turnover at the macro-scale, it was also evident that the contribution of the smaller and larger scales was also significant. Thus it can be concluded that all scales contribute to high nematode genus or species diversity and as Vanreusel et al. (2010) state, habitat heterogeneity is a major factor structuring nematode communities at seep environments.

4.4 Is there evidence for a specialized fauna?

The results from the present study support previous observations that species composition at cold seeps and mud volcanoes is not consistent, since not always the same species (or genera) were dominant or subdominant. The relatively high number of species that were restricted to a single habitat (unique species: 20.3 %) suggests a high potential for endemism. It should be mentioned, however, that in the present study, as with most other deep-sea ecological surveys, nematode species identifications were done as putative or "working" species (e.g. *Sabatieria sp.1*, *Sabatieria sp.2*, etc.), a practice that does not allow a comparative analysis with assemblages from

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different locations, except in the case when identifications are performed by the same research group. For this reason, identifications at the genus level is perhaps more appropriate. However, genus-level identification is also problematic since most genera have the potential to colonize a variety of deep-sea substrata and appear to be distributed worldwide (Vanreusel et al., 2010). Nevertheless, although species identification is more labour-intensive, expensive and requires considerable expertise, it probably remains the preferable way since meiofaunal diversity is expected to vary strongly with taxonomic resolution. In a comprehensive review on the worldwide distribution of deep-sea nematode species, Miljutin et al. (2010) reported that, from a total of 638 valid species, only 46 (7.2 %) could be considered as cosmopolitan. This also suggests that there is a great potential for endemism in the deep-sea, including cold seeps and mud volcanoes. To date, the few studies reporting nematode distribution patterns from cold-seep areas at the species level are rather confusing. At the Håkon Mosby Mud Volcano, Van Gaever et al. (2009b) found one single nematode species (*Halomonhystera disjuncta*) thriving with extremely high numbers in the bacterial mats. Since *H. disjuncta* has been often reported from shallow waters, it was initially suggested that it was capable of successfully colonizing different habitats. However, molecular analysis indicated that *H. disjuncta* may actually belong to a complex of cryptic species impossible to distinguish morphologically (Derycke et al., 2007; Fonseca et al., 2008). Another such example is the case of *Sabatieria mortenseni*, a species which is well known from shallow areas but also from the REGAB cold seep in the Gulf of Guinea, where it was dominant (Van Gaever et al., 2009a). The dominant species of the present study (*Sabatieria sp.4*) strongly resembles *Sabatieria mortenseni* (A. De Groote, personal communication, 2012) suggesting that remote seeps located at completely different geographic areas are possibly interconnected. However, based on the above example of *Halomonhystera disjuncta*, and without any clear molecular evidence, it is more likely that *Sabatieria sp.4* will be another cryptic species of the *Sabatieria mortenseni* complex. On the other hand, *Aponema sp. 1*, that strongly dominated the reduced sediments of Amsterdam, does not look similar to any of the valid *Aponema* species. Moreover, it

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is never reported in high densities from the deep-sea; thus, it is very likely that this particular species is endemic to the reduced sediments of Amsterdam. In addition, many of the other putative species identified from the reduced samples appear to be new, suggesting possible endemism to seep environments at the species level. All the above examples clearly suggest that it is very difficult to draw conclusions on endemism of cold-seep fauna based exclusively on morphology and without the use of molecular techniques.

5 Conclusions

The comparison of meiofaunal communities in two different mud volcanoes in the eastern Mediterranean showed high densities at Amsterdam, probably reflecting a higher seepage activity at the Anaximander mud field (Amsterdam mud volcano) compared to the Olimpi area (Napoli mud volcano). On the other hand, biomass values were one order of magnitude higher at Napoli, the main reason being an apparent shift in nematode size-spectra towards longer and wider animals at Napoli.

In contrast to the standing stock, the effects on nematode biodiversity were variable. At some seep habitats, species richness was significantly high while at others only few species were encountered. Although the highest species turnover was observed at the level of habitats (e.g. sampling at a scale of 10 s to 100 s of meters), all sampling scales (e.g. from ms to 100s of kms) were found to significantly contribute to species richness; thus enhancing the biodiversity of nematode communities.

This study further supports previous observations that species composition of nematode communities is not consistent between seeps. The dominance of *Aponema sp.1* and *Sabatieria sp.4* at different habitats and the high relative abundance of *Manganonema* at one station suggests that nematode communities are patchy distributed and that each habitat may be characterised by a completely different assemblage, depending on specific environmental characteristics.

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The high morphological similarity between *Sabatieria sp.4* and *Sabatieria mortenseni*, a cosmopolitan species which has been reported from many different substrata including mud volcanoes, and the dissimilarity of *Aponema sp.1* with any of the known *Aponema* species, together with the high densities of *Manganonema* at one of the stations, clearly suggests that both cosmopolitanism and endemism are highly possible in cold-seep environments.

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Table 2. Meiofauna relative abundance (%) and densities (individuals per 10 cm² ± SD) at the different habitats of the two mud volcanoes and the control station (*n* = 1 for *Lamellibrachia* field and periphery, the reduced sediment of Amsterdam as well as the control site).

| Area | Habitat type | Nematoda | Copepoda | Annelida | Mollusca | Others | No of Taxa |
|-----------------------|-----------------------------------|---------------|-----------|-----------|-------------|-----------|------------|
| | Abundance (%) | | | | | | |
| Amsterdam | <i>Lamellibrachia</i> field | 90.6 | 3.8 | 2.3 | 0.3 | 2.9 | 12 |
| | <i>Lamellibrachia</i> periphery | 94.5 | 3.1 | 1.1 | 0.5 | 0.9 | 13 |
| | Mussel bed | 82.4 | 5.4 | 2.1 | 2.9 | 7.3 | 14 |
| | Summit | 84.6 | 10.8 | 1.9 | 0.5 | 2.2 | 15 |
| Napoli | Reduced sediment | 93.4 | 4.5 | 0.8 | 0.7 | 0.6 | 9 |
| | <i>Lamellibrachia</i> field | 95.7 | 2.6 | 0.9 | 0.1 | 0.6 | 8 |
| | <i>Lamellibrachia</i> periphery | 89.3 | 7.6 | 1.4 | 0.1 | 1.6 | 10 |
| | Mussel bed | 88.1 | 7.9 | 1.9 | 0.1 | 1.9 | 10 |
| Anaximander mud field | Mussel bed periphery | 89.9 | 6.1 | 1.3 | 0.2 | 2.6 | 10 |
| | Control | 90.8 | 4.4 | 1.8 | 0.7 | 2.2 | 9 |
| | Density (ind/10 cm ²) | | | | | | |
| Amsterdam | <i>Lamellibrachia</i> field | 1359 | 57 | 35 | 5 | 44 | |
| | <i>Lamellibrachia</i> periphery | 1622 | 52 | 18 | 9 | 15 | |
| | Mussel bed | 1127 (± 1002) | 57 (± 23) | 33 (± 37) | 19 (± 17) | 48 (± 44) | |
| | Summit | 735 (± 108) | 91 (± 48) | 16 (± 1) | 4 (± 6) | 19 (± 8) | |
| Napoli | Reduced sediment | 1357 | 65 | 12 | 10 | 9 | |
| | <i>Lamellibrachia</i> field | 560 (± 150) | 16 (± 10) | 6 (± 2) | 0.3 (± 1) | 3 (± 2) | |
| | <i>Lamellibrachia</i> periphery | 476 (± 212) | 33 (± 19) | 6 (± 3) | 1 (± 1) | 9 (± 8) | |
| | Mussel bed | 313 (± 116) | 29 (± 15) | 8 (± 6) | 0.2 (± 0.3) | 6 (± 0.3) | |
| Anaximander mud field | Mussel bed periphery | 780 (± 605) | 58 (± 55) | 10 (± 7) | 2 (± 2) | 24 (± 23) | |
| | Control | 108 | 5 | 2 | 1 | 3 | |

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Table 3. Relative abundance of nematode genera contributing on average with more than 1 % to the total abundance.

| Genus | Amsterdam | | | | | Napoli | | | | Anaximander mud field Control |
|---------------------------|----------------------|--------------------------|------------|--------|------------------|----------------------|--------------------------|------------|----------------------|-------------------------------|
| | Lamellibrachia field | Lamellibrachia periphery | Mussel bed | Summit | Reduced sediment | Lamellibrachia field | Lamellibrachia periphery | Mussel bed | Mussel bed periphery | |
| <i>Sabatieria</i> | 24.2 | 16.1 | 24.9 | 18.7 | 40.6 | 49.6 | 10.2 | 2.0 | 20.2 | 1.4 |
| <i>Aponema</i> | 4.4 | 24.9 | 13.7 | 3.4 | 51.2 | 10.7 | 3.3 | 4.9 | 11.0 | 12.9 |
| <i>Metalinhomoeus</i> | 2.0 | 15.7 | 5.5 | 8.2 | 3.5 | 13.1 | 1.9 | 4.0 | 3.1 | 0.0 |
| <i>Leptolaimus</i> | 2.0 | 1.1 | 6.7 | 8.6 | 2.0 | 1.5 | 5.4 | 4.5 | 4.2 | 3.8 |
| <i>Thalassomonhystera</i> | 4.4 | 2.7 | 4.5 | 4.0 | 0.0 | 0.0 | 3.8 | 3.1 | 4.2 | 11.9 |
| <i>Microlaimus</i> | 1.6 | 9.2 | 8.0 | 4.4 | 0.0 | 0.4 | 4.4 | 2.2 | 2.9 | 1.4 |
| <i>Daptonema</i> | 3.6 | 1.5 | 1.2 | 6.2 | 0.0 | 9.1 | 3.1 | 3.4 | 2.1 | 1.9 |
| <i>Molgolaimus</i> | 6.5 | 0.0 | 0.4 | 5.2 | 0.0 | 0.3 | 8.1 | 4.3 | 5.0 | 0.0 |
| <i>Desmodora</i> | 11.7 | 0.8 | 2.5 | 0.0 | 0.0 | 1.1 | 2.5 | 3.1 | 4.4 | 0.0 |
| <i>Syringolaimus</i> | 0.0 | 0.0 | 1.6 | 1.4 | 0.4 | 1.2 | 4.0 | 11.4 | 2.5 | 3.3 |
| <i>Acantholaimus</i> | 0.4 | 1.9 | 1.4 | 1.8 | 0.0 | 0.1 | 3.5 | 6.7 | 0.6 | 5.2 |
| <i>Anticomma</i> | 10.5 | 0.0 | 2.0 | 7.6 | 0.0 | 0.0 | 0.4 | 0.2 | 0.4 | 0.5 |
| <i>Paramonhystera</i> | 1.6 | 1.1 | 1.6 | 2.8 | 0.0 | 8.9 | 0.8 | 1.8 | 0.4 | 1.4 |
| <i>Viscosia</i> | 5.6 | 1.1 | 3.3 | 2.6 | 0.4 | 0.0 | 0.8 | 1.8 | 1.0 | 0.5 |
| <i>Marylynnia</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 11.6 | 4.0 | 0.0 |
| <i>Halalaimus</i> | 1.6 | 1.9 | 1.4 | 0.2 | 0.0 | 0.0 | 2.7 | 2.0 | 1.2 | 3.8 |
| <i>Cyartonema</i> | 1.6 | 2.7 | 0.8 | 3.6 | 0.0 | 0.1 | 0.8 | 1.1 | 1.0 | 1.0 |
| <i>Setosabatieria</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 6.5 | 0.0 | 5.4 | 0.0 |
| <i>Tricoma</i> | 1.2 | 2.7 | 1.8 | 0.4 | 0.0 | 0.0 | 1.5 | 0.7 | 1.5 | 1.4 |
| <i>Pareudemoscolex</i> | 0.0 | 4.2 | 0.4 | 1.4 | 0.0 | 0.0 | 0.6 | 0.2 | 3.7 | 0.0 |
| <i>Manganonema</i> | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 1.5 | 2.2 | 0.0 | 6.2 |
| <i>Terschellingia</i> | 0.8 | 2.3 | 0.0 | 0.2 | 0.0 | 2.5 | 2.5 | 0.7 | 1.0 | 0.0 |

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Table 4. Diversity indices (Hill numbers) of nematode communities from different habitats of Amsterdam and Napoli mud volcanoes and the control station.

| Area | Habitat type | N_0 | N_1 | N_2 | N_{inf} |
|-----------|---------------------------------|----------------|--------------------|--------------------|------------------|
| Amsterdam | <i>Lamellibrachia</i> field | 47 | 24.6 | 13.6 | 4.9 |
| | <i>Lamellibrachia</i> periphery | 42 | 16.7 | 9.3 | 4.1 |
| | Mussel bed | 43 (\pm 19) | 21.9 (\pm 16.7) | 13.4 (\pm 10.6) | 4.9 (\pm 2.2) |
| | Summit | 46 (\pm 8) | 24.9 (\pm 8.5) | 15.5 (\pm 6.9) | 6 (\pm 2.7) |
| | Reduced sediment | 12 | 2.9 | 2.3 | 1.9 |
| Napoli | <i>Lamellibrachia</i> field | 15 | 4.9 | 3.6 | 2.6 |
| | <i>Lamellibrachia</i> periphery | 53 (\pm 20) | 31.2 (\pm 17.7) | 19.4 (\pm 12) | 6.3 (\pm 2.4) |
| | Mussel bed | 56 (\pm 1) | 30.9 (\pm 6) | 20.4 (\pm 6.9) | 8.7 (\pm 3.7) |
| | Mussel bed periphery | 48 (\pm 25) | 25.2 (\pm 19.8) | 15.8 (\pm 13.5) | 6.4 (\pm 4.7) |
| Control | Control | 56 | 36.5 | 24.3 | 7.8 |

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Table 5. Beta and delta diversity based on Jaccard dissimilarity. Dissimilarity increases from 0 to 1.

| | <i>Lamellibrachia</i> field | <i>Lamellibrachia</i> periphery | Mussel bed | Reduced sediment | Summit | Mussel bed periphery | All seep habitats |
|---------------------------------|--------------------------------|------------------------------------|---------------|---------------------|--------|-------------------------|----------------------|
| β -diversity | | | | | | | |
| Within habitats | | | | | | | |
| Amsterdam | | | 0.74 | | 0.52 | | |
| Napoli | 0.59 | 0.72 | 0.63 | | | 0.75 | |
| Between habitats | | | | | | | |
| Amsterdam | | | | | | | |
| <i>Lamellibrachia</i> field | | | | | | | |
| <i>Lamellibrachia</i> periphery | 0.63 | | | | | | |
| Mussel bed | 0.58 | 0.55 | | | | | |
| Reduced sediment | 0.87 | 0.83 | 0.86 | | | | |
| Summit | 0.64 | 0.61 | 0.52 | 0.84 | | | |
| Control | 0.76 | 0.69 | 0.59 | 0.87 | 0.66 | | 0.59 |
| Napoli | | | | | | | |
| <i>Lamellibrachia</i> field | | | | | | | |
| <i>Lamellibrachia</i> periphery | 0.73 | | | | | | |
| Mussel bed | 0.76 | 0.46 | | | | | |
| Mussel bed periphery | 0.74 | 0.47 | 0.54 | | | | |
| Control | 0.79 | 0.65 | 0.60 | | | 0.66 | 0.63 |
| δ -diversity | | | | | | | |
| Between mud volcanoes | | | | | | | |
| | 0.74 | 0.65 | 0.58 | | | | 0.41 |

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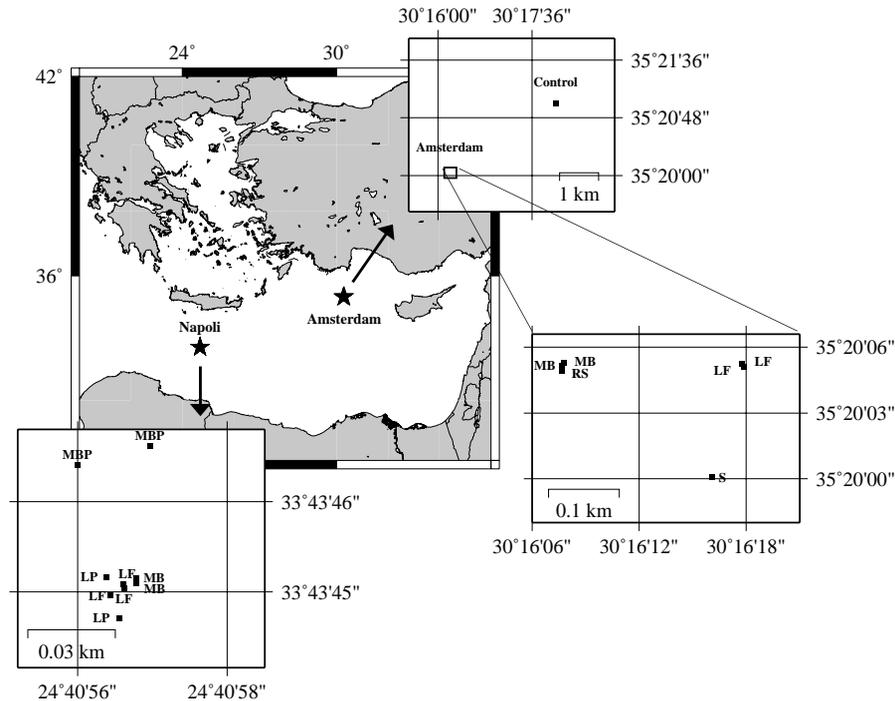


Fig. 1. General map of the Eastern Mediterranean Sea with the location of the two mud volcanoes. Smaller maps show detailed positions of the different microhabitats: LF: *Lamellibrachia* field; LP: *Lamellibrachia* periphery; MB: Mussel bed; MBP: Mussel bed periphery; S: Summit; RS: Reduced sediments.

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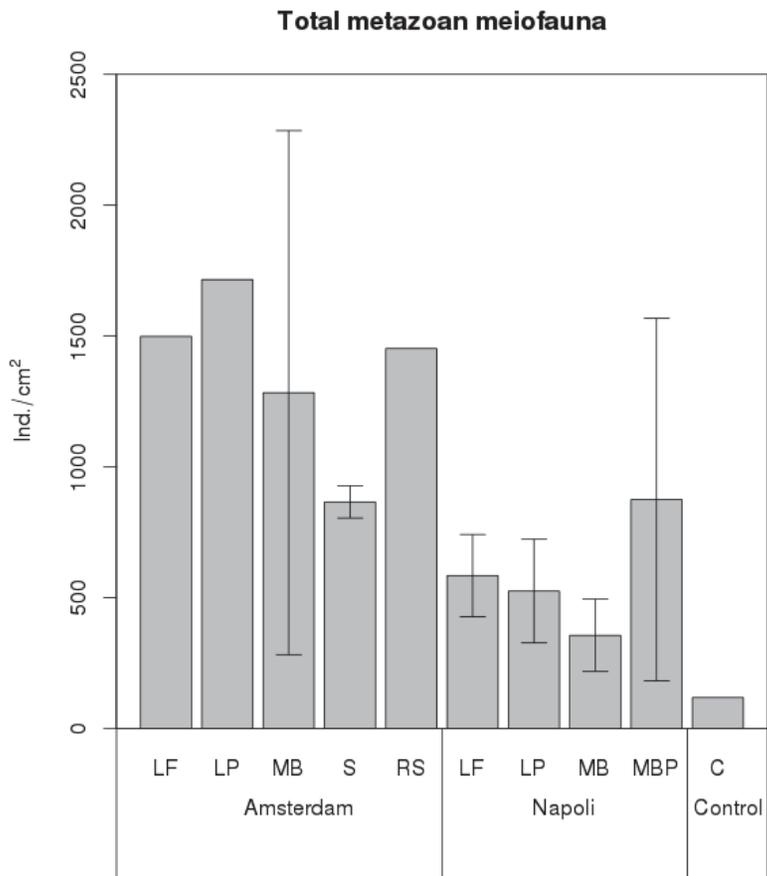


Fig. 2. Total metazoan meiofauna (individuals per 10 cm²) per habitat at the two mud volcanoes and the control station. LF: *Lamellibrachia* field; LP: *Lamellibrachia* periphery; MB: Mussel bed; S: Summit; RS: Reduced sediments, MBP: Mussel bed periphery; C: Control.

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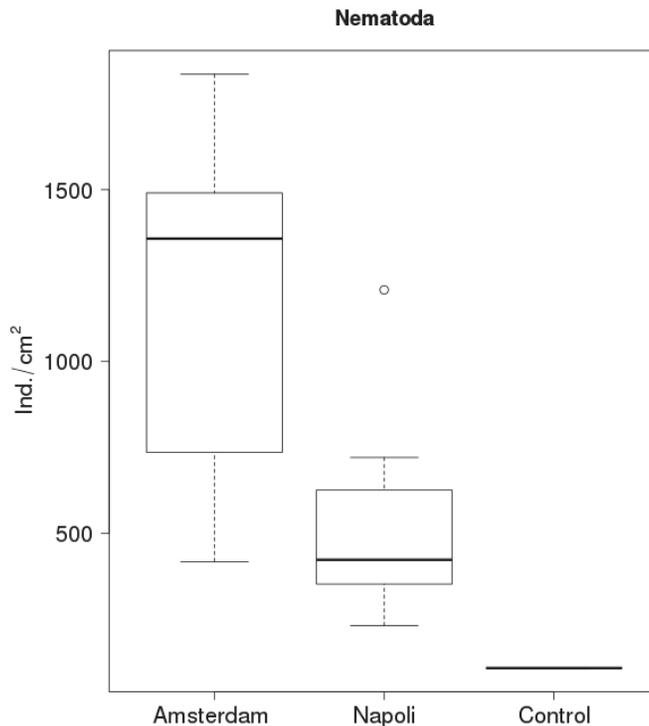


Fig. 3. Box-plot showing differences in nematode densities between the Amsterdam and Napoli mud volcanoes and the control station.

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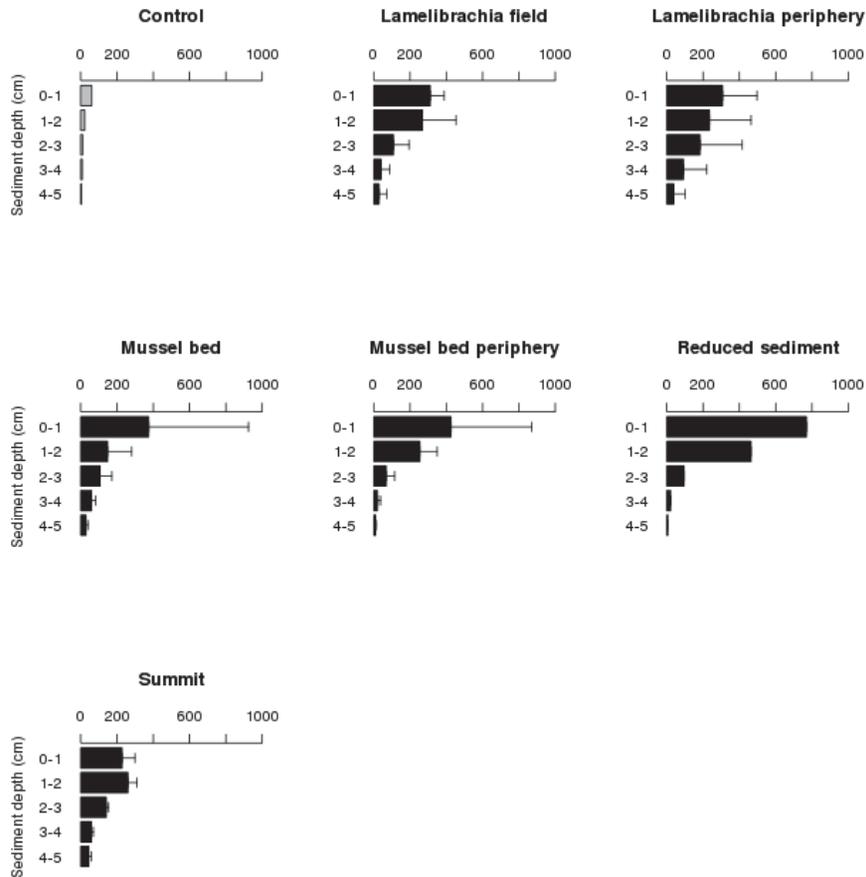


Fig. 4. Vertical distribution (individuals per 10 cm²) of nematodes for the different habitats of the two mud volcanoes and the control station. For habitats studied at both volcanoes, average values are presented.

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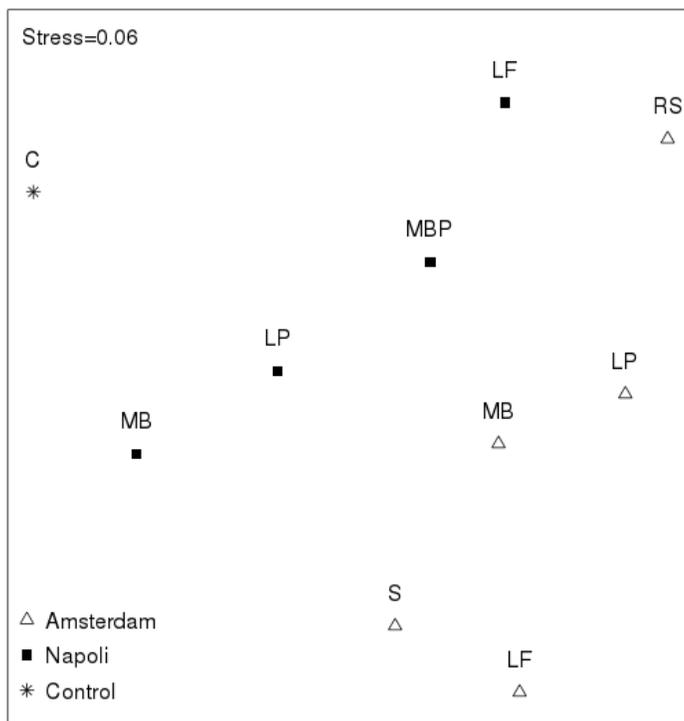


Fig. 5. Non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity of none transformed nematode species data from the two mud volcanoes and the control station. LF: *Lamellibrachia* field; LP: *Lamellibrachia* periphery; MB: Mussel bed; S: Summit; RS: Reduced sediments, MBP: Mussel bed periphery; C: Control.

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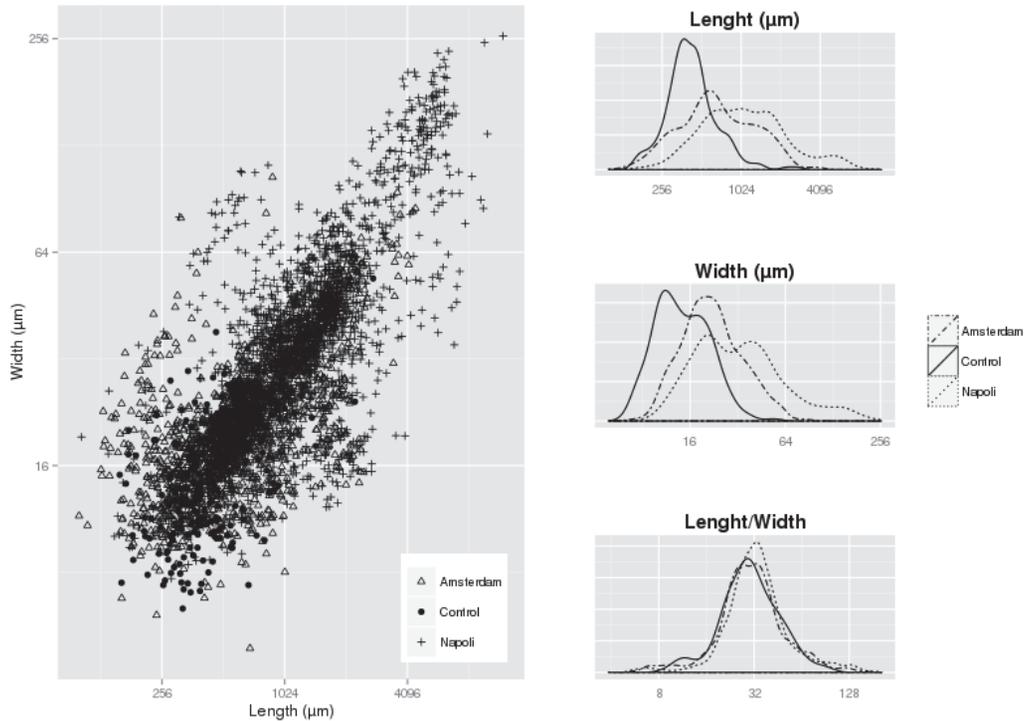


Fig. 6. Morphometric data of individual nematodes. Large panel shows length–width relationship at the three sampling sites. Smaller panels show frequency distributions of length, width and length : width ratio.

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