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Rapid colonisation by nematodes on organic and inorganic substrata deployed at the deep-sea Lucky Strike hydrothermal vent field (Mid-Atlantic Ridge)

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Abstract Despite the fragmented nature of hydrothermal vent (HV) fields, nascent vent sites are rapidly colonized by a pool of regional species. While succession of large animals at vents is relatively well established, we lack information on the associated meiofauna, in particular, on nematodes. The aim of the present study is to investigate the process of colonisation after 9 months of organic (wood and bone) and inorganic (slate) substrata by nematode assemblages deployed at the Eiffel Tower hydrothermal edifice on the Lucky Strike vent field on the Mid-Atlantic Ridge (MAR), at varying distances from visible hydrothermal activity. Abundance, biomass and diversity of colonising nematodes were compared with the results from an earlier similar two-year experiment. Near the vents, nematodes preferred inorganic substrata while in areas not influenced by vent activity, organic substrata were preferred. Nematode females dominated at almost all sites while numerous females at the ovigerous stage and juveniles were reported near the vent emissions, suggesting that nematode populations reproduce well after just 9 months. Our nine-month experiment on the MAR showed that the type of substratum influenced significantly the composition of colonising nematodes, while after two years, the community structure was instead influenced by hydrothermal activity.

Keywords Nematodes · Colonization substrata · Wood · Bone · Slate · Mid-Atlantic Ridge · Hydrothermal vents

Introduction

Hydrothermal vents (HVs) are extreme environments where percolating cold seawater (~2–4 °C) penetrates the fractured oceanic crust. Being heated and enriched with reduced chemicals, the hydrothermal fluid emerges from the seafloor at temperatures up to 400 °C (Van Dover 2000). Hydrothermal organisms are adapted to the presence of extreme environmental conditions (high concentrations of reduced compounds, heavy metals and radionucleides, low oxygen level, and elevated temperatures; Sarradin et al. 1999; Charmasson et al. 2009). Despite the apparent harshness of the environment, HVs are hot-spots of high productivity and biomass when compared to the surrounding deep-sea benthos (Cuvelier et al. 2014). In addition, hydrothermal habitats are ephemeral and they have a longevity that is directly related to volcanic, tectonic and magmatic processes (Van Dover 2000). As hot fluid venting is transient, hydrothermal vent sites have ephemeral lifespans ranging from years (e.g. HV 9°50′ N at the East Pacific Rise (EPR); Shank et al. 1998; Lutz et al. 2008) to decades or, exceptionally, centuries [e.g., the Mid-Atlantic Ridge, (MAR); Humphris et al. 2002]. Distances between HV fields are variable (up to hundreds of kilometres; Murton et al. 1994; German et al.

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1996). In addition to their remoteness, hydrodynamic and physical barriers (e.g., faults) can contribute to the isolation of hydrothermal vent fauna (Desbruyères et al. 2001).

Despite the significant degree of separation between HV fields, nascent vent sites are rapidly (months/years) colonized by a pool of regional species, even when the nearest populated hydrothermal vent is situated several kilometres away (Tunnicliffe et al. 1997; Shank et al. 1998; Tsurumi and Tunnicliffe 2001; Marcus et al. 2009). In 2006, a pilot study was set out to obtain better comprehension of community dynamics, colonization and recruitment patterns of local fauna around the Eiffel Tower edifice on the Lucky Strike vent field. For this, a series of six substrata (wood and slate) were deployed for two years before recovery (Cuvelier et al. 2014, and references therein). Results of this pilot study suggested that the local physical and chemical water conditions (mainly temperature and chemical compound concentrations) rather than the substratum type were the most important factors influencing the settlement and colonization of local fauna, although biological interactions appeared to be important (Cuvelier et al. 2014). Previous colonisation experiments at vents using inorganic substrata showed that colonisation patterns were influenced by a complex interaction between the composition of the surrounding community, variability in microhabitat conditions and biological interactions (Mullineaux et al. 2003; Govenar and Fisher 2007; Kelly et al. 2007). Gaudron et al. (2010) and Cuvelier et al. (2014) performed the first studies that also included the deployment of organic substrata (wood) in chemosynthetic environments and revealed that organic substrata attracted both chemosynthetic fauna as well as other opportunistic species.

Whilst mega- and macrofauna in HVs have been studied since their discovery, the ecology of meiofaunal organisms has only recently been included in vent studies (Tsurumi et al. 2003; Zekely et al. 2006a, b; Limén et al. 2007; Gollner et al. 2007, 2010a, b; Copley et al. 2007; Sarrazin et al. in press). Several HV habitats, from inactive bare basalts (Gollner et al. 2010b) and sediments (Vanreusel et al. 1997) to diffuse flow areas colonized by macrofaunal assemblages (Zekely et al. 2006a, c), host meiofaunal communities characterized by low abundance and diversity, linked with the abiotic and biotic conditions of the habitat (Gollner et al. 2010b; Zekely et al. 2006a, c; Degen et al. 2012). In most cases, nematodes and copepods are the most abundant meiofaunal organisms (Vanreusel et al. 2010; Zeppilli et al. submitted). The nematodes identified in vents can belong to families and genera already known from non-vent habitats (Dinet et al. 1988; Vanreusel et al. 1997; Zekely et al. 2006c; Sarrazin et al. in press). In some hydrothermal vents such as at the North Fiji Basin (Vanreusel et al. 1997) and Izu-

Ogasawara Arc in the western North Pacific Ocean (Setoguchi et al. 2014), none of the nematode species found in hydrothermal sediments occurred in the surrounding abyssal areas. Conversely, at the EPR, several nematode vent species have been found in abyssal sediments surrounding hydrothermal vent fields (Gollner et al. 2010b, 2015).

While succession of large animals at vents is relatively well observed (Sen et al. 2014), we know much less on the associated meiofauna and, in particular, on nematodes (Gollner et al. 2013). A study on mussel beds of different ages (4 to >20 years) showed that nematodes were less abundant and diverse at younger sites (Copley et al. 2007). Volcanic eruptions would negatively impact nematodes that may require long periods to colonize a newly lava-flooded area (Gollner et al. 2013). Recolonisation of vents by nematodes following volcanic eruptions appears to be strongly linked to the survival of populations in nearby undisturbed topographic features (Gollner et al. 2013).

The aim of the present study is to investigate the process of colonisation of organic and inorganic substrata by nematode assemblages at deep-sea HVs. Two types of organic substrata (wood and bone) and one type of inorganic substratum (slate) were deployed at the Eiffel Tower hydrothermal edifice on the Lucky Strike vent field on the Mid-Atlantic Ridge (MAR) for 9 months, at varying distances from visible hydrothermal activity. Wood and bone were chosen due to their organic nature, their wide distribution in the oceans (Smith and Baco 2003; Schwabe et al. in press) and their potential as evolutionary stepping stones for hydrothermal vent colonization (Distel et al. 2000; Lorion et al. 2009). As inorganic substratum, slate was chosen due to its basalt-like smoothness and inert characteristics. We investigated abundance, biomass and diversity of colonising nematodes and compared our data with the two-year experiment performed at the same location by Cuvelier et al. in 2014 to answer the two following questions:

i)   Are nematodes mostly influenced by the type of substratum or by environmental constraints (e.g., hydrothermal activity) at an early stage of colonisation (9 months)?
ii) Are there differences in the nematode community after 9 months and 2 years for the same substrata and locations?

Materials and methods

Study site

The Lucky Strike vent field is situated on the MAR, south of the Azores (Fig. 1). It is a large vent field with a central lava
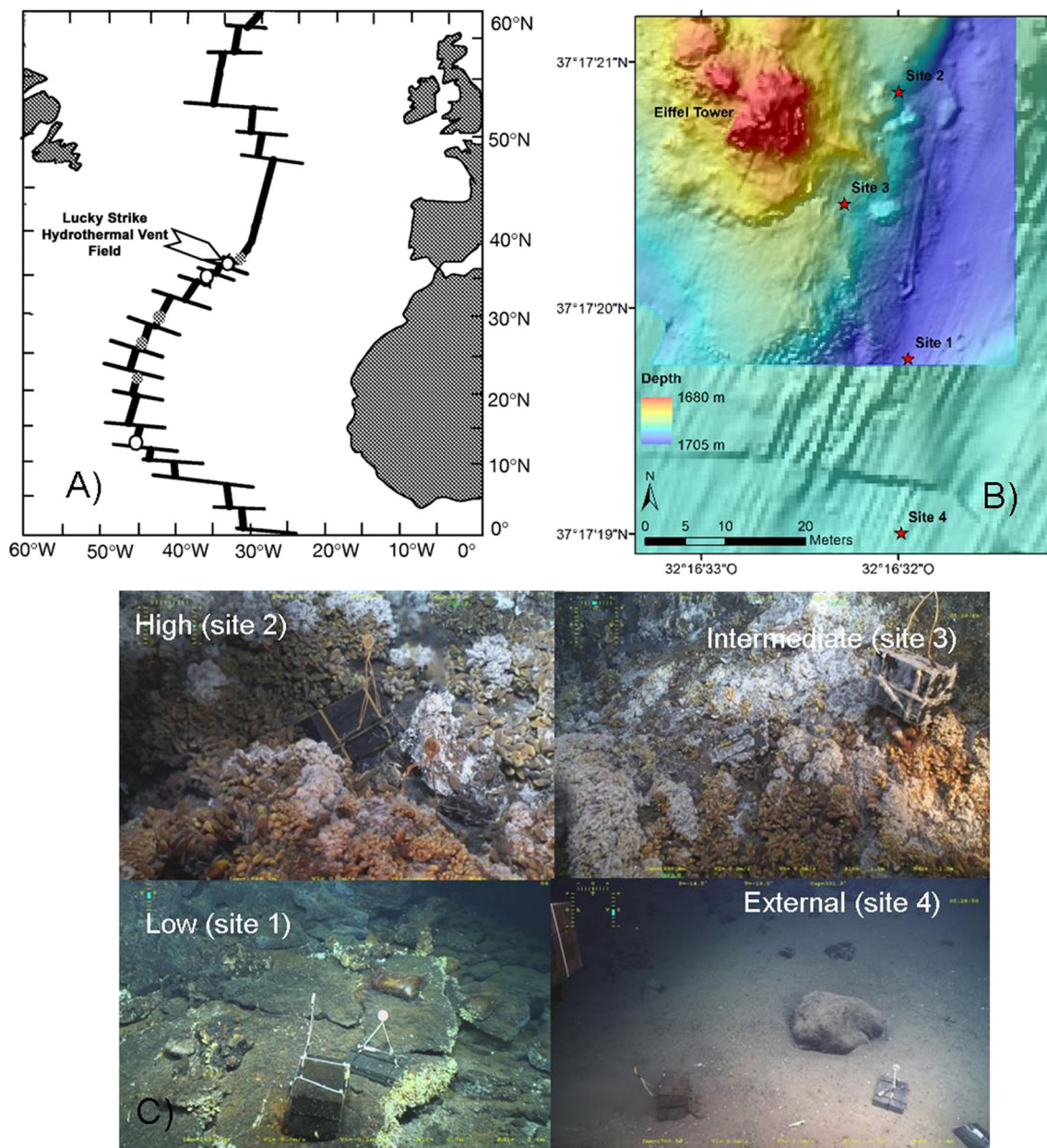
Fig. 1 Location of the Lucky Strike vent field on the Mid-Atlantic Ridge (MAR) at 37°17.59 N, 32°169 W (**a**). The locations of the sites where different substrata were deployed around the Eiffel Tower edifice (**b**) are reported. On each locality, slate, wood, and bone were deployed (**c**)

lake with an ~200-m diameter, surrounded by three volcanic cones (Ondréas et al. 2009). Several hydrothermal edifices can be found around the lava lake. The Eiffel Tower edifice is a well-defined active edifice 11 m high and one of the most-visited sites within the Lucky Strike vent field. It has been the focus of ecological research over the last ten years (e.g., Van Dover et al. 1996; Comtet and Desbruyeres 1998; Desbruyères et al. 2001; Cuvelier et al. 2009; Cuvelier et al. 2011a; Cuvelier et al. 2012; Sarrazin et al. in press; Matabos et al. in press), and also recently in regards to short-term (Sarrazin et al. 2014) and long-term (Cuvelier et al. 2011b) temporal variation studies.

Experimental design and sample collection

Three types of substrata, one inorganic (basalt-like slate, A) and two organic (wood, B and bone, C), were deployed during the MOMARSAT 2010 cruise (October 2010 on the research vessel Pourquoi Pas?), on four different sites (1 to 4) up and around the Eiffel Tower edifice (Fig. 1 and Table 1), at varying distances from visible hydrothermal activity. The sites chosen correspond to those reported by Cuvelier et al. (2014), with the exception of one additional external site (site 4) ca. 25 m from the Eiffel Tower edifice. Therefore, substrata at sites 1 and

Table 1 Location, depth and temperature of the sites at the Eiffel Tower edifice (MAR) where different substrata were deployed in 2010 and recovered in 2011 (avg.=average). Fluid inputs in percentage were calculated using the formula provided by Sarradin et al. (2009) for the Eiffel Tower edifice (%=0.314T−1.38)

Site	Emission	Latitude (N)	Longitude (W)	Depth (m)	T°C Avg.	Min.	Max.	% Fluid Inputs
2	High	37° 17.3484′	32° 16.5333′	1699	5.7	4.3	7.7	0.41
3	Intermediate	37° 17.3404′	32° 16.5379′	1698	5.2	4.4	6.7	0.25
1	Low	37° 17.3299′	32° 16.5325′	1704	4.9	4.3	6.7	0.16
4	External	37° 17.3181′	32° 16.5331′	1705	4.6	4.3	4.9	0.06

3 were deployed at the base of the south side of the Eiffel Tower, at respective distances of 3 m and 4–5 m from the edifice. Substrata 1 (A, B and C; Fig. 1c) were placed in the visibly least populated and least hydrothermal active region (low hydrothermal influence site; Fig. 1c). Substrata 3 (A, B and C) were put on a crack with diffuse venting, bordered by *Bathymodiolus azoricus* mussels and microbial mats (intermediate hydrothermal influence site; Fig. 1c). Substrata 2 (A, B and C) were situated at site 2 on a spur of the Eiffel Tower edifice towards the north–west (high hydrothermal influence site; Fig. 1c). Finally, substrata 4 (A, B and C) were situated at site 4 between two hydrothermal edifices 69 m from site 2, 52 m from site 3 and 27 m from site 1. Only substrata A2, B2 and C2 were located directly on the edifice and were situated in the most densely populated area of the three deployment sites, within less than half a meter from various fluid exits, surrounded by dense *Bathymodiolus azoricus* assemblages. Each slate substratum was equipped with an autonomous NKE ST 6000 temperature probe, which measured temperature every 15 minutes (Table 1). Temperature is used here as a proxy for hydrothermal influence and a percentage of hydrothermal fluid input at each site was calculated using the formula proposed by Sarradin et al. (2009) for the same area (Table 1). Each colonization substrata was measured to evaluate the surface available for colonization. 3D imaging techniques were used to reconstruct the substrata using a calibration grid and photographs taken at different angles before their deployment (coll. M. Aron, ISEN engineering school). The surface available for colonization in each substratum is reported in Table 2.

Nine months later, in July 2011, the substrata were recovered during the MOMARSAT 2011 cruise. However the bones situated at sites 1 and 4 had disappeared. We suspect that large predators are responsible as sharks were observed several times during our substratum deployments. Both substrata deployment and recovery were carried out with the remotely operated vehicle (ROV) Victor6000. Upon recovery, all substrata were placed in individual isotherm sampling boxes and brought to the surface.

Nematode abundance and biomass

On board, the faunal samples were pre-sieved through 1000-, 250- and 20-μm mesh nets. Samples were preserved in seawater-buffered formalin (10 %). In the lab, nematodes were counted under a stereomicroscope. The nematode biomass was calculated from the biovolume, which was estimated from all specimens per replicate using the Andrassy formula ($V=L \times W^2 \times 0.063 \times 10^{-5}$, with body length, L, and width, W, expressed in μm; Andrassy 1956). The carbon contents were identified as 40 % of the dry weight (Feller and Warwick 1988). Nematode measurements were taken using an AxiozoomV16 stereomicroscope (400× magnification) using the software Zen 2012 (blue edition).

Nematode biodiversity

From each substratum sample, 200 randomly collected nematodes were mounted on slides after formalin–ethanol–glycerol treatment to prevent dehydratation (Danovaro 2010) and identified to the species level according to Platt and Warwick (1983, 1988), Warwick et al. (1998), and the recent literature dealing with new nematode genera and species from the Atlantic Ocean. Unknown species were reported under the name of the genus and then as sp1, sp2 and so on.

NSR was calculated as the total number of species collected for each site. Nematode species diversity (H', using logbase e) was measured using the Shannon–Wiener diversity index, with the evenness as the Pielou index (J). The Margalef diversity index (D) was estimated as $D=(S-1/\ln N)$, where S is the number of nematode species and N is the number of individuals in the sample. In order to facilitate comparison among samples, the expected number of nematode species for a theoretical random sample of 100 individuals, ES (100), was calculated. All indices were calculated using the PRIMER6 software (Plymouth Marine Laboratory, UK; Clarke 1993).

The trophic diversity of the nematodes was determined by analysing trophic groups, as reported by Wieser (1953). The nematodes were divided into four groups, as follows: (i) no buccal cavity or a fine tubular one, as selective (bacterial) feeders (1A); (ii) large, but unarmed, buccal cavity, as non-

Table 2 Size and respective colonisable surface area of each substratum deployed in 2010 and recovered in 2011

Substrate		Size of the substratum (mm)			Colonisable surface area (mm^2)
Name	Kind	X	Y	Z	
A1	Slate	215	309	63	173,045
A2	Slate	241	326	54	175,441
A3	Slate	211	309	54	166,149
A4	Slate	219	307	54	170,398
B1	Wood	193	321	220	228,018
B2	Wood	218	302	224	304,895
B3	Wood	235	305	219	297,343
B4	Wood	195	292	197	285,344
C1	Bone	244	342	194	226,916
C2	Bone	155	263	122	139,992
C3	Bone	211	348	162	180,714
C4	Bone	269	335	17	171,150

selective deposit feeders (1B); (iii) buccal cavity with scraping tooth or teeth epistrate or epigrowth feeders (2A); and (iv) buccal cavity with large jaws, as predators/omnivores (2B). The index of trophic diversity (ITD) was calculated as Θ, where $\Theta = g_1^2 + g_2^2 + g_3^2 \ldots + g_n^2$, and g is the relative contribution (in terms of number of specimens) of each trophic group to the total number of individuals, and n is the number of trophic groups (Heip et al. 1985). For $n=4$, Θ ranges from 0.25 (highest trophic diversity; i,.e. the four trophic groups each account for 25 % of the nematode abundance) to 1.0 (lowest diversity; i.e., when one trophic group accounts for 100 % of the nematode abundance). Nematode trophic structure was calculated based on the nematode biomass matrix.

The maturity index (MI) of nematode populations was calculated from life strategies (r - k) of the nematodes for which these strategies are known. In order to identify colonization strategies, nematodes are divided into "colonizers" (comparable to r-strategists, characterized by a short life cycle, high colonization ability, and tolerance to disturbance, e.g., eutrophication, and anoxybiosis) and "persisters" (k-strategists with a low reproduction rate, long life cycle, and low colonization ability and tolerance to disturbance; the list of species with different life strategies is reported by Bongers et al. 1991). The MI was calculated according to the weighted mean of the individual genus scores: $MI = \Sigma\, v\,(i)\, X\, f\,(i)$, where v is the c–p value (colonisers–persisters; ranging from 1, i.e., only opportunistic colonizers, to 5, i.e., only persisters) of the genus i (Bongers et al. 1991) and f (i) is the frequency of that genus.

Statistical analyses

Premised on the fact that these experiments are characterised by a lack of replicates, statistical analyses in this study are limited to a principal component analysis (PCA) and a non-parametric multivariate multiple regression analysis.

The Bray-Curtis similarity matrix (with data square-root transformed) was used for the PCA, which allowed visualization of between-site and between-substrata variations in the nematode assemblages after 9 months (PRIMER6 software, Plymouth Marine Laboratory, UK; Clarke 1993).

We evaluated the relationship after 9 months between nematode abundance, biomass, diversity (as nematode species composition, NSR, ITD and MI) and environmental variables (temperature and fluid inputs reported as high, medium, low, absent) and type of substrata (slate, wood and bone) conducting a non-parametric multivariate multiple regression analysis (DistLM: distance-based linear model) using the PERMANOVA + add-on package for PRIMER6 software (McArdle and Anderson 2001; Anderson et al. 2008). This method analyses and models the relationship between a multivariate data cloud and one or more predictor variables. It is based on a resemblance matrix and uses permutations rather than the restrictive Euclidean distance and normality assumptions which underlie the standard approach to linear modeling. For total abundance, biomass and diversity indices, the Euclidean distance was used as a resemblance measure, whereas for species composition, the analysis was based on Bray-Curtis dissimilarities. Forward selection was carried out and the adjusted R^2 was selected as the criterion to enable fitting of the best explanatory environmental variables in the model (Anderson et al. 2008). The results are provided as marginal and sequential tests. The marginal test revealed how much each variable explains when taken alone, ignoring all other variables. Following the results of this test, a sequential test was performed which examined whether the addition of that particular variable contributes significantly to the explained variation (Anderson et al. 2008).

Results

Environmental conditions

The highest average temperature was recorded at the high emission site (5.7 °C), followed by the intermediate (5.2 °C), and low emission sites (4.9 °C; Table 1). The average temperature at the external site was 4.6 °C. Variation between the maximal and minimal temperatures was highest at the high emission site (3.4 °C) and lowest at the external site (0.6 °C). At a given site, temperature can be used as a proxy of hydrothermal influence since it correlates well with the chemical characteristics of the fluids (Sarradin et al. 1999; Sarradin et al. 2009). Using the formula provided by Sarradin et al. (2009) we calculated the % of fluid inputs (Table 1). At site 2, the % of fluid inputs was 0.41, 0.25 at site 3, 0.16 at site 1 and 0.06 at the external site. Furthermore, a recent study on the Eiffel Tower edifice (De Busserolles et al. 2009) showed positive correlations between temperature and total dissolved sulphide and iron concentrations. For example, an increase of 0.5° leads to 3 times more total dissolved sulphide, 120 times more total dissolved iron, and a pH reduction of 0.26 (De Busserolles et al. 2009).

Nematode abundance on substrata recovered after 9 months

The highest nematode density was reported in the wood located at the external site while the lowest was found on the wood located at the low emission site, with 242,006.1 and 381.5 ind m^{-2}, respectively (Table 3). The abundance decreased with decreasing fluid emission in slate, with values 10 times lower at the external site, from 17,641.3 to 1250.0 ind m^{-2} (Table 3). Concerning the two recovered bones (C3 and C2), the abundance was higher at the intermediate site than at the high emission site, 4792.1 and 2807.3 ind m^{-2}, respectively (Table 3).

Nematode biomass on substrata recovered after 9 months

Nematode biomass showed a similar pattern as that of abundance with the highest value on wood of the external site and the lowest on wood of the low emission site, respectively 9680.2 and 13.4 μgC m^{-2} (Table 3). High biomass values were also reported on the wood located at the high emission site (2310.8 μgC m^{-2}, Table 3) due to the dominance of *Oncholaimus sp.1* in this site. The average biomass for individuals of this species (3 μgC m^{-2}) was 60 times higher than the average biomass reported for the other nematodes species (0.05 μgC m^{-2}). On slate, the biomass decreased with decreasing fluid emission, from 829.1 to 116.3 μgC m^{-2} (Table 3). Concerning the two recovered bones, the biomass was higher

Table 3 Nematode abundance, biomass and diversity indices of all investigated substrata recovered after 9 months. Nematode species richness (NSR), the Margalef (D), Pielou (J) and Shannon–Wiener (H') diversity indexes, the expected species number ES(100), a maturity index (MI) and an index of trophic diversity (ITD) are presented. The highest values for each parameter are indicated in bold. F: females, GF: gravid females, M: males, J: juveniles, NA: not available

Substratum	Emission	Name	Abundance (ind/m²)	Abundance (ind/10 cm²)	Biomass (μgC/m²)	Biomass (μgC/10 cm²)	NSR	D	J'	ES(100)	H'	MI	ITD	F (%)	GF (%)	F + GF (%)	M (%)	J (%)
Slate	High	A2	17,641.3	17.6413	829.1	0.8291	8.0	1.2	0.2	5.3	0.7	3.9	0.9	22	**22**	44	25	31
	Intermediate	A3	12,338.3	12.3383	728	0.728	11.0	1.8	0.4	8.5	1.4	3.7	0.7	25	13	38	37	25
	Low	A1	3819.8	3.8198	209.4	0.2094	8.0	1.3	0.4	5.9	1.1	3.4	0.7	29	4	32	21	**46**
	External	A4	1250	1.25	116.3	0.1163	11.0	2.1	0.4	10.6	1.4	3.5	0.7	27	**22**	49	41	10
Wood	High	B2	757.6	0.7576	2310.8	2.3108	1.0	0.0	–	1.0	0.0	**4.0**	**1.0**	36	21	**57**	29	14
	Intermediate	B3	995.5	0.9955	29.9	0.0299	2.0	0.2	0.4	2.0	0.4	1.2	0.9	**48**	10	**57**	5	38
	Low	B1	381.5	0.3815	13.4	0.0134	10.0	2.4	**0.9**	10.0	**2.8**	2.2	0.4	38	19	56	34	9
	External	B4	**242,006.1**	**242.0061**	**9680.2**	**9.6802**	5.0	0.8	0.8	4.9	1.8	1.6	0.6	27	7	34	**55**	12
Bone	High	C2	2807.3	2.8073	98.3	0.0983	7.0	1.2	0.7	6.4	1.9	1.1	0.8	37	15	52	26	22
	Intermediate	C3	4792.1	4.7921	273.1	0.2731	**14.0**	**2.5**	0.4	**10.9**	1.7	1.6	0.6	34	18	52	26	21
	Low	NA																
	External																		

at the intermediate site (C3) than at the high emission site (C2), 273.1 and 98.3 μgC m^{-2}, respectively (Table 3).

Nematode diversity in substrata recovered after 9 months

Overall, 24 nematode species belonging to 20 genera and 12 families were identified. In slate substrata, Draconematidae was the dominant family. This family increased its dominance with increasing vent emission (from 76 to 93 % of the total nematode abundance, from external to high emission sites, respectively; Fig. 2), while the family Monhysteridae increased its dominance with decreasing vent emission (from 4 to 16 % of the total nematode abundance, from high to low emission sites, respectively; Fig. 2). On wood substrata, Monhysteridae was the dominant family, accounting for 42–93 % of the total nematode abundance, except for the high emission site (site 2) where Oncholaimidae totally dominated the community (Fig. 2). The family Microlaimidae was found only on the wood located in the low and external sites, accounting for 20 and 30 % of the total nematode abundance, respectively (Fig. 2). Bones were largely dominated by Monhysteridae (92 and 74 % of the total nematode abundance in high emission and intermediate sites, respectively; Fig. 2), followed by Microlaimidae at the high emission site (6 %) and Draconematidae at the intermediate site (9 %). The genus *Cephalochaetosoma* dominated slate substrata (75–90 %), while *Halomonhystera* dominated bone substrata (71–92 %; Table 4). On wood, *Oncholaimus* dominated the site with highest hydrothermal activity (site 2, 100 %), *Halomonhystera* dominated the intermediate and low emission sites (sites 3 and 1, 42–93 %), while *Thalassomonhystera* dominated the external site (site 4, 61 %; Table 4).

NSR was highest on the bone recovered from the intermediate emission site (14 species) and lowest on the wood at the high emission site (1 species). On slate, 8 species were identified at the intermediate emission and external sites and 11 species were found at the high and low emission sites (Table 3). On wood, species richness was very low at the high and intermediate emission sites (1 and 2 species, respectively),

while at the low emission and external sites, 10 and 5 species were respectively identified (Table 3). Considering each set of substrata, the highest species richness was recorded at the intermediate site (17 species), while the lowest was found at the high emission site (12 species).

The number of "exclusive" species reported at each site increased with decreasing influence of vent emission from 0 at the high emission site to 3 at the external site. Considering the substratum, seven species were exclusively reported on slate (representing 29 % of the total richness), two species were exclusively reported on wood (8 %) and only one on bone (4 %, Fig. 3). At the high emission site, only one species (*Oncholaimus sp.1*) was shared by the three substrata and two species were shared between slate and bone (*Cephalochaetosoma sp.1* and *Halomonhystera sp.1;* Fig. 3). At this site, five species were exclusively encountered on slate and four on bone. At the intermediate emission site, two species were shared by the three substrata (*Cephalochaetosoma sp.1* and *Halomonhystera sp.1*) and five species were shared by slate and bone; while three species were exclusively reported on slate and six on bones (Fig. 3). At the low emission site, slate and wood shared five species, respectively showing five and three exclusive species (Fig. 3). At the external site, only 1 species was shared by wood and slate (*Calomicrolaimus sp.1*), while slate and wood, respectively, reported 11 and 4 exclusive species (Fig. 3).

On slate, deposit feeders, including selective (1A) and non-selective feeders (1B) dominated the trophic structure of nematodes, representing 90–95 % of the total nematode abundance, with selective feeders (1A) decreasing with increasing vent emission (Fig. 4). On wood, non-selective feeders (1B) dominated at all sites (49–93 %), except at the high emission site, where predators/omnivores (2B) represented 100 % of the nematode community. On bone, non-selective feeders (1B) dominated the high (92 %) and intermediate sites (75 %). The ITD increased with increasing influence of vent emissions on all types of substrata (Table 3). The MI was particularly low on bone (1.1–1.6), and always high, between 3.5–3.9 on slate (Table 3). Wood substrata showed a low MI

Fig. 2 Nematode family composition found on the investigated substrata recovered after 9 months
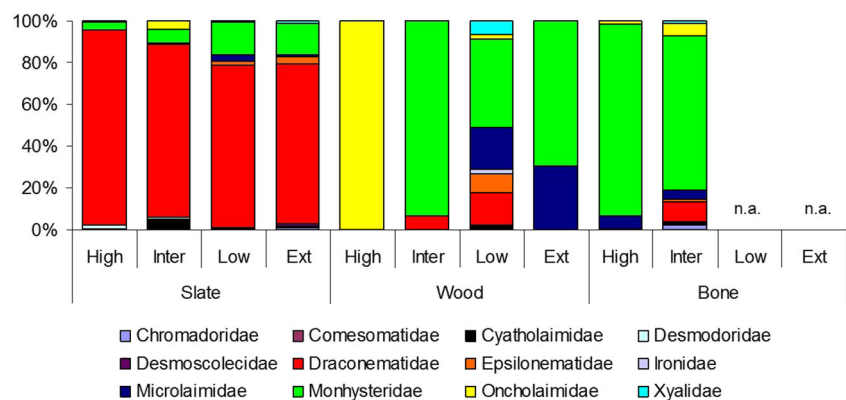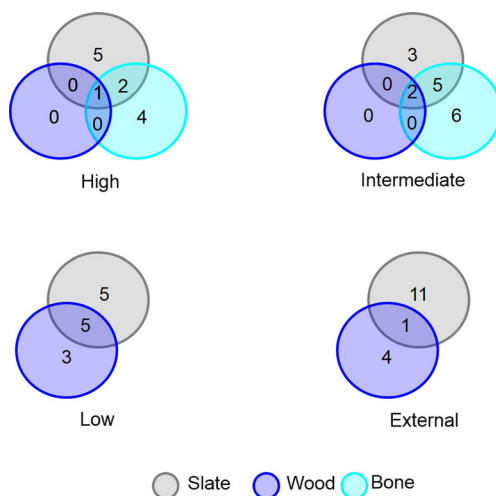
Table 4 List of nematode species encountered in the investigated substrata recovered after 9 months and relative abundance (%). Highest values are highlighted in bold

| Nematode species	Slate				Wood				Bone	
	High A2	Intermediate A3	Low A1	External A4	High B2	Intermediate B3	Low B1	External B4	High C2	Intermediate C3
Aponema sp1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.5	0.0	0.6
Calomicrolaimus sp1	0.0	0.0	0.0	0.9	0.0	0.0	0.0	10.4	0.7	2.9
Cephalochaetosoma sp1	**90.0**	**76.8**	**77.4**	**74.5**	0.0	6.6	15.6	0.0	0.7	9.2
Chromadorita sp1	0.3	0.7	0.0	0.9	0.0	0.0	0.0	0.0	0.0	2.3
Cobbia sp1	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	1.1
Desmodora marci	1.3	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Desmoscolex sp1	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Dinetia sp1	3.3	5.6	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Epsilonema sp1	0.3	0.7	1.4	1.9	0.0	0.0	8.9	0.0	0.0	1.1
Epsilonema sp2	0.0	0.0	0.5	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Halomonhystera sp1	3.7	6.4	15.7	15.1	0.0	**93.4**	**22.2**	0.0	28.9	**72.4**
Halomonhystera sp2	0.0	0.0	0.0	0.0	0.0	0.0	20.0	20.0	16.3	0.6
Halomonhystera sp3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**46.7**	0.6
Metacomesoma sp1	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metepsilonema sp1	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Microlaimus sp1	0.0	0.0	3.2	0.0	0.0	0.0	20.0	1.5	5.2	1.1
Molgolaimus sp1	0.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oncholaimus sp1	0.7	4.1	0.5	0.0	**100.0**	0.0	2.2	0.0	1.5	6.3
Paracanthonchus sp1	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Paracanthonchus sp2	0.0	0.4	0.0	0.9	0.0	0.0	2.2	0.0	0.0	0.6
Paracyatholaimus sp1	0.0	2.2	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syringolaimus sp1	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0
Thalassomonhystera vandoverae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	49.6	0.0	0.0
Theristus sp1	0.0	0.0	0.0	0.9	0.0	0.0	4.4	0.0	0.0	0.0

Fig. 3 Venn diagrams reporting the number of nematode species for each investigated site encountered after 9 months. The number of species reported in each circle represents the number of species exclusively found on one substratum type. The number of species reported in the intersections represents the shared species

value at the intermediate emission site and a very high value of 4 at the high emission site (Table 3). It increased with increasing influence of vent emissions on slate (from 3.5 to 3.9), while it showed an opposite pattern on bone (1.1 and 1.6 at the high and intermediate sites, respectively; Table 3). The nematode sex ratio is reported in Table 3. Females dominated at all sites and on all substrata (32–57 %), except on the wood of the external site, where males dominated (55 %). An important number of gravid females were observed in all samples (4–22 %) with the highest number on slate at the high emission site where juveniles were also particularly abundant (representing up to 46 % of the nematode community).

Nematode colonization after 9 months compared with the results from the 2 years experiment

The abundance of nematodes decreases with decreasing influence of vent emissions on slate recovered both after 9 and 24 months (Fig. 5). Higher abundance was always found after

Fig. 4 Nematode trophic structure of colonisation substrata recovered after 9 months. 1A: selective (bacterial) feeders; 1B: non-selective deposit feeders; 2A: epistrate feeders; 2B: predators/ omnivores
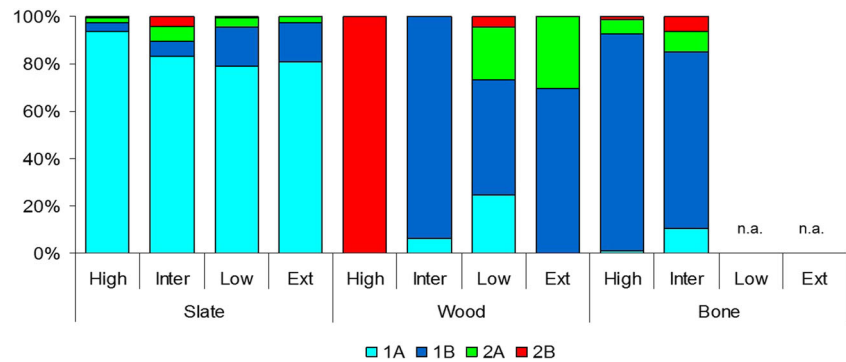
9 months. On wood, the intermediate emission site showed the highest abundance value after 9 months and the lowest after 24 months (Fig. 5; for details, see Cuvelier et al. 2014). The nematode family composition on slate and wood from different sites is reported in Fig. 6. After 9 months, Draconematidae dominated slate while on wood, Oncholaimidae dominated at high emission sites and Monhysteridae at intermediate and low emission sites. After 2 years, Draconematidae dominated at high and low emission sites both on slate and wood while we reported the co-dominance of Draconematidae, Microlaimidae and Monhysteridae at the intermediate emission site both on slate and wood (Fig. 6; for details, see Cuvelier et al. 2014).

Statistical results

PCA analyses revealed that the wood situated in the high emission site (B2) was strongly separated from the other substrata (Fig. 7), due to the presence of *Oncholaimus sp.1*. PCA of the species composition data also revealed a discrimination between inorganic substrata (slate) and organic substrata (with the exception of B2; Fig. 7).

The DistLM analysis showed the environmental variables that were best correlated to the observed distribution patterns (Table 5). The environmental data available did not explain the differences in nematode abundance, biomass and diversity (expressed as NSR). However, differences in nematode species composition were significantly explained by the type of substrata (22 %). The type of substrata also significantly

explained 60 % of the differences in the MI, while temperature explained 50 % of the observed differences in the ITD; nevertheless, feeding types were different on slate and wood at high emission sites.

Discussion

Nematode colonisation patterns on organic and inorganic substrata recovered after 9 months

Nematode abundances reported in this study are consistent with available data from other Atlantic deep-sea vents (Zekely et al. 2006a; Cuvelier et al. 2014; Sarrazin et al. in press; Table 6), confirming that nematodes are part of hydrothermal vent communities (Sarrazin et al. in press). To our knowledge, information on hydrothermal vent nematode biomass is reported exclusively by two studies (Vanreusel et al. 1997; Gollner et al. 2007). In the deep-sea HV of the North Fiji Basin, the mean weight was between 0.23 and 0.35 μg wet wt in active HVs and 0.15 μg wet wt in inactive sites (Vanreusel et al. 1997). In the present study, nematode mean wet weight can reach values 100 times higher than in Vanreusel et al. 1997, with a peak of 30.5 μg wet wt in the wood of the most active site (site 2). On the EPR, nematode biomass was 20 times lower than the values observed in the present study (Gollner et al. 2007). Biomass values reported in this study are for most samples consistent with values reported from a nematofauna investigated in a seamount close to the

Fig. 5 Nematode abundance on colonisation substrata (slate and wood) recovered after 9 months and after 2 years
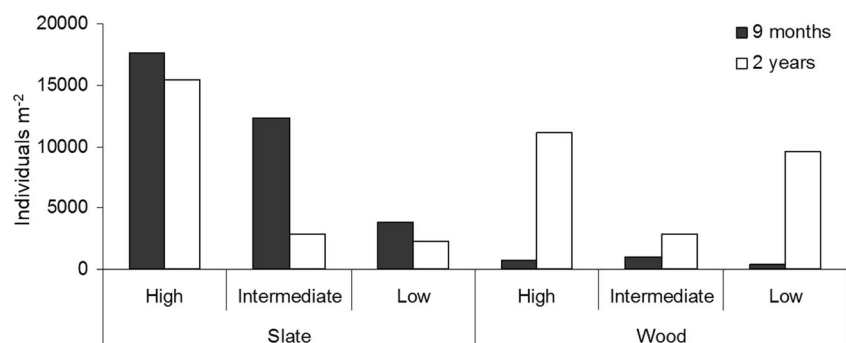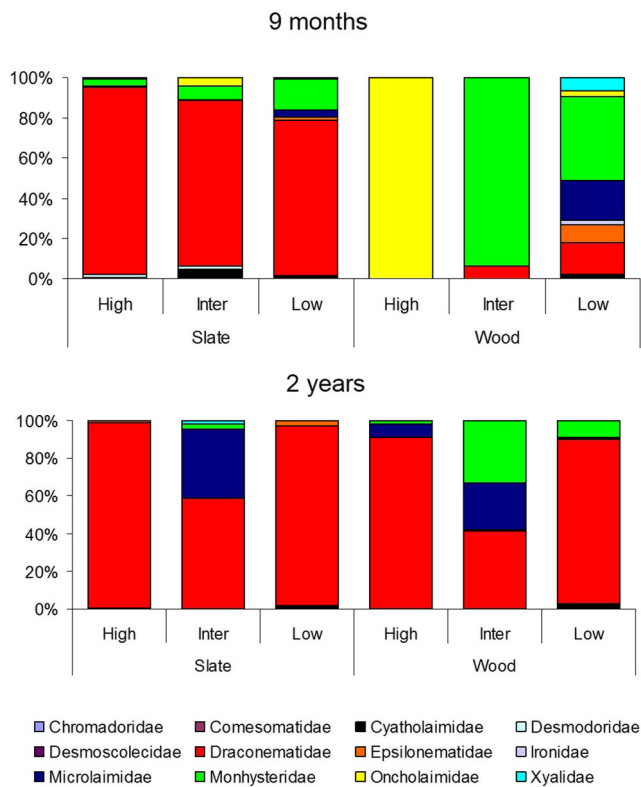
Fig. 6 Nematode family composition of colonisation substrata (slate and wood) recovered after 9 months and after 2 years

Lucky Strike hydrothermal vent field (Condor Seamount; Zeppilli et al. 2013). The same trend observed for abundance was observed for nematode biomass in inorganic substrata with an increase of values with increasing influence of vent emission. An opposite trend (increase of biomass with decreasing vent emission) was observed on bone, while on wood, we observed values of biomass 100 times higher in the highest emission and external sites than in the others. At the high emission site, this unexpected peak of nematode biomass is due to the dominance of the big nematode *Oncholaimus sp.1*, which can reach 7–8 mm in length as adults. This nematode is 10 times longer than the nematode lengths reported by Vanreusel et al. (1997) in the deep-sea HV of the North Fiji Basin. Big nematodes belonging to the Oncholaimidae family were reported worldwide in association with shallow water vent emission (Zeppilli and Danovaro 2009) but rarely reported in deep-sea hydrothermal vents and always in very low abundance (Vanreusel et al. 2010; Sarrazin et al. in press). This study showed that, in some cases, deep-sea HVs can support rich nematode communities in terms of standing stocks (both abundance and biomass), and further studies are needed to reveal the spatial distribution of nematodes in this peculiar ecosystem. The high biomass values on wood at the external site are explained by the high densities of small colonizers such as Monhysterids and *Microlaimus*. *Microlaimus* is known as an early colonizer of

disturbed or new habitats (Lee et al. 2001; Muthumbi et al. 2004; Van Gaever et al 2009). It colonized the wood in very high abundances without any vent emission influence.

The nematodes identified in this study belong to families and genera already known from the Lucky Strike HV field (Zekely et al. 2006a; Cuvelier et al. 2014; Sarrazin et al. in press), with exception for the genus *Oncholaimus* that was for the first time reported in deep-sea Atlantic HVs, considering both meiofauna and macrofauna studies. *Cephalochaetosoma* and *Halomonhystera*, reported as the dominant genera in the nematofauna associated with mussel beds in the MAR (Sarrazin et al. in press), dominated slate and bone recovered after 9 months (Table 4). Nematodes reported from the MAR (Zekely et al. 2006a; Cuvelier et al. 2014; Sarrazin et al. in press), the North Fiji Basin (Vanreusel et al. 1997), and other Pacific hydrothermal sites (Flint et al. 2006; Zekely et al. 2006a; Gollner et al. 2007, 2010b) were dominated by few nematode taxa. The richest nematode diversity was reported in soft sediments associated with *Bathymodiolus* mussels from the North Fiji basin with over 30 genera identified (Vanreusel et al. 1997). In this study, we observed a total of 24 species belonging to 20 genera, with a local species diversity varying between 1 and 14 species, confirming the trend of low evenness described by Sarrazin et al. (in press). Similar to Gollner et al. (2013), we observed that active vent sites were dominated by a few generalists, while rare and exclusive species increased with distance from a vent's influence.

Cephalochaetosoma sp.1 and *Halomonhystera sp. 1* were both able to colonise slate and bone at the high emission site and all substrata at the intermediate emission site. *Oncholaimus sp.1* was able to colonise all the substrata investigated in this study, while this species dominated the wood at the high emission site, reaching high biomass values for the total nematode community. The genus *Oncholaimus* is known to tolerate extreme geothermal and hypersaline conditions and high sulphide concentrations in shallow hydrothermal vents (Gerlach and Riemann 1973; Thiermann et al. 1994). The species *Oncholaimus campylocercoides,* found in HVs of the Aegean Sea as well as in brackish waters in the Baltic and Black Seas (Thiermann et al. 1994, 1997), can produce sulphur-containing droplets when exposed to hydrogen sulphide (Thiermann et al. 1994), potentially reducing the 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). Our study showed that the genus *Oncholaimus* (only occasionally found in deep-sea vents; Vanreusel et al. 1997) could colonise deep-sea HVs, becoming an important component (in term of abundance and biomass) of vent fauna.

The fact that females dominated almost at all sites, and that all substrata near the vent emission harboured high numbers of juveniles and females at the ovigerous stage supports the idea

Fig. 7 PCA of investigated colonisation substrata recovered after 9 months
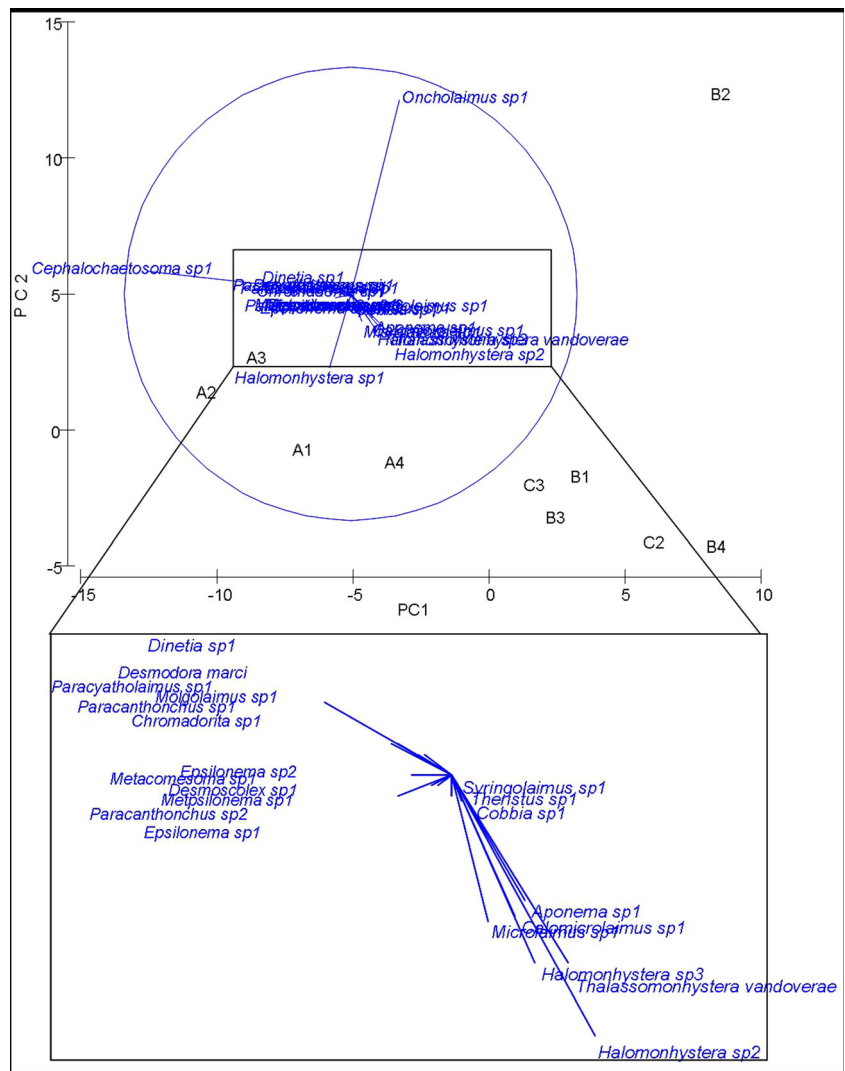
that nematodes were reproducing and, thus, represented a well-established population. The discovery of a high

abundance of copepodites and nauplii in deep-sea HVs was recently reported by Sarrazin et al. (in press), reconsidering

Table 5 Results of the DistLM analysis (Selection criterion: adjusted R^2) highlighting the effect of different variables on nematode abundance, biomass and diversity in substrata recovered after 9 months (NSR: Nematode Species Richness; SS: sum of squares; F: F statistic; P: probability level; ***$P<0.001$; **$P<0.01$; *$P<0.05$; ns: not significant)

	Variables	SS	F	p		Variance (%)
Nematode abundance	Vent emission	1.2E+10	2.5121	0.17	ns	24
Nematode biomass	Vent emission	1.25E+07	1.4796	0.299	ns	16
	Temperature	1.01E+07	1.227	0.318	ns	13
Nematode species richness	Temperature	13.404	0.77315	0.385	ns	9
Nematode species composition	**Substrata**	**5233.9**	**2.2405**	**0.038**	*	**22**
	Vent emission	3328.4	1.5168	0.162	ns	14
	Temperature	2713.8	1.2875	0.282	ns	11
Index of trophic diversity	**Temperature**	**0.16424**	**8.0736**	**0.02**	*	**50**
	Substrata	2.09E-02	1.0312	0.348	ns	6
Maturity index	**Substrata**	**7.5348**	**12.072**	**0.015**	*	**60**
	Temperature	1.5186	3.0594	0.123	ns	12

Table 6 Summary of studies investigating nematodes at deep-sea HVs (modified from Vanreusel et al. 2010; NA: not available)

Vent location		Water depth (m)	Nematode abundance (ind./10 cm²)	Dominant genera	Note	References
N Pacific	North Fiji Basin	1990	3–42 (ind./10 cm³)	Leptolaimus, Molgolaimus, Monhystera, Desmodora, Marylinnia, Acantholaimus		Vanreusel et al. 1997
N Pacific	Pacificlheya Ridge	1393	NA	Neochromadora, Desmolaimus, Monhysterida		Shirayama 1992
N Pacific	Myojin Knoll caldera	1300	1–30.9	Pseudochromadora, Microlaimus, Pareudesmoscolex		Setoguchi et al. 2014
EPR	Buckfield	2480	1–2	Thalassomonhystera, Monhysteridae, Theristus		Zekely et al. 2006a
EPR	Buckfield	2480	1–2	Thalassomonhystera		Zekely et al. 2006c
EPR	Riftia	2500	1–7	Thalassomonhystera		Gollner et al. 2007
EPR	Tica	2500	16–946	Thalassomonhystera		Gollner et al. 2007
EPR	Biovent, East Wall, Train Station	2500	22–116	Thalassomonhystera		Copley et al. 2007
EPR	Rehu Marka, Oasis, Animal Farm, Buddha's Place	2581–2690	50–72	Thalassomonhystera, Anticoma		Copley et al. 2007
EPR		2491–2690	51.3	Halomonhystra, Thalassomonhystera		Flint et al. 2006
EPR	Guaymas	1800–2600	NA	Desmodoridae		Dinet et al. 1988
EPR	Juan de Fuca Ridge	1500	NA	Paracanthonchus, Leptolaimus, Chromadorida, Linhomoeidae		Limén et al. 2007
EPR		2500	1–946	NA		Gollner et al. 2010b
EPR		2500	0–1432	Thalassomonhystera, Neochromadora, Halomonhystera, Monhysterida	Colonisation experiment	Gollner et al. 2013
MAR	Lucky Strike	1700	2.3–15.5	Cephalochaetosoma, Halomonhystera, Dinetia, Microlaimus	Colonisation experiment	Cuvelier et al. 2014
MAR	Lucky Strike	1700	6.2–685.4	Cephalochaetosoma, Halomonhystera		Sarrazin et al. in press
MAR	Snake Pit	3492	28	Thalassomonhystera, Anticoma, Diplopeltula		Zekely et al 2006a

previous assumptions suggesting that copepod larval stages were located outside active hydrothermal areas. Furthermore, we observed that the genus *Halomonhystera* showed an ovoviviparous reproduction strategy. The ovoviviparous reproductive mode has already been described for Monhysteridae living in harsh environmental conditions (Van Gaever et al. 2006), but it is being reported for the first time for deep-sea HVs.

Nematode studies at the EPR revealed that the diversity of nematodes changed along a gradient of fluid emission (over a temperature gradient of >50 °C; Gollner et al. 2010b), emphasizing the role of environmental conditions. In this study, we observed that after 9 months, nematode communities were mainly influenced by the type of substratum and that environmental conditions appeared to play a minor role (Fig. 7 and Table 5), even though small variations in temperature correspond to significant variations of associated chemical conditions and hydrothermal fluid inputs (Sarradin et al. 2009). Also, trophic diversity showed marked differences among the different types of substratum with selective deposit feeders dominating the inorganic slate and non-selective deposit-feeders dominating the organic wood and bone substrata.

Comparison of nematode colonisation patterns on organic and inorganic substrata after 9 months and 2 years

Information about succession of nematodes in deep-sea HVs are poor (Gollner et al. 2013). After a volcanic eruption at the EPR, Gollner et al. (2013) showed that nematodes required long periods to colonize new lava-flooded areas in greater numbers and richness. Conversely, in our study we observed that nematodes colonised both organic and inorganic substrata in high abundance and diversity after just 9 months. The study of Gollner et al. (2013) investigated the recovery after a disturbance that affected a whole region, killing almost all nematodes present in this area. Nematodes migrating from distant areas may have required longer time to recolonize the perturbed areas (Gollner et al. 2013). In Lucky Strike experiments (9-month and 24-month sets), nematode abundance on inorganic substrata increased with increasing vent emissions (Fig. 5). Only after 2 years did we observe higher nematode abundances on organic substrata than on inorganic substrata (15 times higher at the high emission site and 30 times higher at the low emission site). This preliminary study suggests that inorganic substrata were preferred by colonising nematodes in the early succession stage, while organic substrata required a long term to host well-established nematode communities. We can hypothesize that opportunistic colonisers are successful during the early colonisation processes selecting organic substrata, but they experienced mortality shortly after settling due the extreme condition of this site.

Similar to what was observed by Gollner et al. (2013), we observed that the most abundant species during early succession were also the dominant species in this area (*Cephalochaetosoma sp.1* and *Halomonhystera sp. 1*; Sarrazin et al. in press). The only exception in our study was the presence of *Oncholaimus sp. 1*, dominant on the wood of the high emission site recovered after 9 months and never reported before in Lucky Strike HV nematofauna. This species was not found after 24 months.

Investigating the nematode family composition in substrata recovered after 9 months and 2 years (Fig. 6), we observed that in the former Draconematidae dominated inorganic substrata, while Monhysteridae dominated the organic substrata (with the exception of the high emission site, where Oncholaimidae dominated). After 2 years, we observed differences in nematode composition between sites with different vent emission influence, regardless of the type of substratum (Fig. 6). The 9-month experiment at the MAR showed that the type of substratum significantly influenced the composition of colonising nematodes, while after 2 years, nematode composition was more influenced by hydrothermal activity (Cuvelier et al. 2014).

Conclusions

This study followed the previous pilot deployment of paired wood/slate panels in close proximity of hydrothermal emissions on and around the Eiffel Tower hydrothermal edifice performed by Cuvelier et al. 2014. The most important limitation of these experiments was the lack of replicates, urging caution in the interpretation of the results. The use of large substrata allowed the concurrent colonisation by meio- and macrofauna, allowing biotic interactions to structure the composition of communities. The analysis of nematodes recovered on organic and inorganic substrata deployed at the deep-sea Lucky Strike HV field (MAR) provided answers to the original questions:

i) Nematodes were able to colonise both organic and inorganic substrata in an early colonisation stage (9 months). The most abundant species during early succession correspond to the dominant species in this area (*Cephalochaetosoma sp.1* and *Halomonhystera sp. 1*) with the exception of *Oncholaimus sp. 1*, which was able to colonise all the substrata investigated and dominated the wood at the high emission site, reaching high biomass values. Active vent sites were dominated by a few generalists, while rare and exclusive species increased with distance from the vent. The presence of important numbers of females at the ovigerous stage and juveniles near the vent emission, suggest that nematodes are already well established near the vent emission after 9 months.

ii) Our data suggested that inorganic substrata is preferred by colonising nematodes in the early succession stage, while the establishment of the nematode community required more time to colonise the organic substrata. We observed that after 9 months, Draconematidae dominated inorganic substrata, while Monhysteridae dominated the organic substrata. The 9-month experiment on the MAR showed that the type of substratum significantly influenced the composition of colonising nematodes, while after 2 years, HV activity was the predominant factor regardless the type of substratum.

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