Simple harpacticoid composition observed at deep hydrothermal vent sites on sea knoll calderas in the North-west Pacific

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Abstract

Dirivultid copepods (Siphonostomatoida), one of the most successful meiobenthic organisms found at deep-sea hydrothermal vents, have been the focus of most previous ecological studies among meiofauna in these habitats. The ecology of Harpacticoida, a major benthic copepod group in typical deep-sea floor, however, is not well understood in terms of variations in community structure and controlling factors at venting sites. The spatial heterogeneities in benthic harpacticoid composition and their association with environmental parameters were investigated at hydrothermal vent chimney structures in the calderas of three neighbouring sea knolls (Bayonnaise Knoll, Myojin Knoll and Myojin-sho Caldera) in the western North Pacific. While a previous study had reported the distribution of dirivultids was strongly associated with spatial differences in stable carbon isotopic signatures ($\delta^{13}C$) of organic matter in the detritus on active chimneys in the field, multivariate analyses detected no significant corelation between the parameter and harpacticoid composition in this study. Instead, high associations of the harpacticoid composition with differences in water depth and total organic carbon (TOC) concentration were detected. Ectinosomatidae dominated at vent sites with lower TOC values in the shallowest Bayonnaise Knoll, while they were less prevalent at deeper vent fields in the other knolls, where Miraciidae was the most abundant family. This study indicated the availability of vent chemoautotrophic carbon is not a primary factor controlling the composition of harpacticoids even in the habitats on the hydrothermal vents, but instead by the food amount, regardless of its resources (including marine snow from the sea surface), in the study area.

Introduction

Deep-sea hydrothermal vent ecosystems are unique ecosystems whose energy source is sustained largely by chemoautotrophic microbial production, differing from typical deep-sea ecosystems that are sustained by phytodetritus input (Van Dover, 2000). Organisms inhabiting hydrothermal vent ecosystems have therefore adapted to utilize such chemoautotrophic food sources or have symbiotic relationships with chemoautotrophic microbes (Dubilier *et al.*, 2008). The taxonomic composition of meiofauna at hydrothermal vents has become the focus of attention in recent decades (e.g. Dinet *et al.*, 1988; Shirayama, 1992; Vanreusel *et al.*, 1997, 2010; Tsurumi *et al.*, 2003; Flint *et al.*, 2006; Gollner *et al.*, 2006, 2007, 2010a, 2015a, 2015b; Zekely *et al.*, 2006a, 2006b; Copley *et al.*, 2007; Degen *et al.*, 2012; Cuvelier *et al.*, 2014; Sarrazin *et al.*, 2015; Zeppilli *et al.*, 2015, 2018; Baldrighi *et al.*, 2017; Plum *et al.*, 2017). However, it is still largely unclear how meiofaunal-sized organisms colonize such an environment, due to the lack of fundamental ecological knowledge at a more refined scale. Studies on faunal compositions covering both vent-specific and 'ubiquitous' meiofauna are also required to understand the colonization process at the vent chimney, and environmental selection during that process.

Recently, we investigated spatial variations in meiofaunal composition on active chimney structures in the calderas of three neighbouring sea knolls (Bayonnaise Knoll, Myojin Knoll and Myojin-sho Caldera) on the Izu-Ogasawara Arc, north-western Pacific Ocean (Figure 1). These studies revealed that the meiofaunal communities on the surfaces of active vent chimneys were dominated by benthic copepods, whereas nematodes were the most abundant taxa in the sediments located around chimney bases (Setoguchi *et al.*, 2014; Uejima *et al.*, 2017). Furthermore, spatial differences in order-level copepod taxonomic composition on venting chimney surfaces were significantly correlated with differences in the availability of vent chemoautotrophic carbon. At the sites with higher values of stable carbon isotope ratios ($\delta^{13}C$) of organic matter in the detritus (suggesting a higher contribution of chemoautotrophic bacteria), Siphonostomatoida dominated, mainly *Stygiopontius senokuchiae*, the first species of Dirivultidae found in the area (Uyeno *et al.*, 2018; Watanabe *et al.*, 2021). In contrast, Harpacticoida, another highly abundant copepod taxon, showed decreased frequencies with
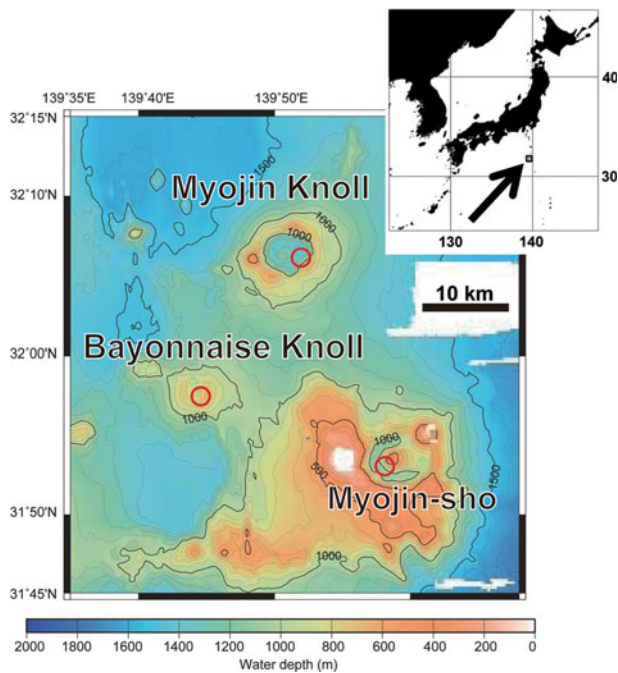
Fig. 1. Map showing locations of Bayonnaise Knoll, Myojin Knoll and Myojin-sho Caldera. Circles indicate the hydrothermal vents investigated.

increasing $\delta^{13}C$ values at vent sites in those knolls (Senokuchi *et al.*, 2018). The $\delta^{13}C$ values of copepod tissues also suggest that dirivultids rely on vent chimney bacteria as their nutritional source (Nomaki *et al.*, 2019). These results strongly suggest that chemoautotrophic food resource availability is the key factor controlling vent copepod distributions, at least at higher taxonomic levels.

Information on harpacticoid communities at deep hydrothermal vent sites had been badly lacking from the north-western Pacific, comparing those in the eastern Pacific and the mid Atlantic (e.g. Tsurumi *et al.*, 2003; Zekely *et al.*, 2006*b*). In this study, we focused on the harpacticoid community composition at the family level on active vent chimneys in the three knolls, as the first step in the investigation of spatial variation of this composition around the hydrothermal area. We examined the degree of similarity in the harpacticoid composition among vent sites in the three knolls in our study area and those in the other provinces on a global scale. The vent sites in each of the investigated knolls were isolated by the high caldera walls that surrounded them. The copepod family Dirivultidae (Siphonostomatoida), a typical vent family, has planktonic nauplii and/or copepodid stages (Ivanenko, 1998; Ivanenko *et al.*, 2007; Gollner *et al.*, 2010*b*), thus enabling wide dispersal via oceanic currents. Harpacticoids, however, usually have direct benthic development, without planktonic nauplius (Huys *et al.*, 1996), and may thus be restricted to expanding their distribution ranges due to the caldera walls functioning as geographic barriers. This results in few similarities in their community composition, even at the family level, between the vent sites in the different knolls. We also investigated the effect of several environmental factors on these harpacticoid compositions around hydrothermal vents on these knolls, including those of food availability, which showed significant effects on the copepod composition at higher taxonomic levels in the study area.

Materials and methods

Meiofaunal sampling and sample processing

The samples used in this study were collected using the research vessel (RV) 'Natsushima' (cruises NT12–10 in 2012, NT13–09 in 2013 and NT14–06 in 2014; all cruises in April), which visited three adjacent knoll-associated calderas with known active hydrothermal vent systems: Bayonnaise Knoll, Myojin-sho Caldera and Myojin Knoll (Figure 1, Table 1). Details of the sampling sites and procedures have been reported previously (Senokuchi *et al.*, 2018; Nomaki *et al.*, 2019). In brief, samples were collected using the remotely operated vehicle (ROV) 'Hyper-Dolphin'. Detritus was collected from aggregations of polychaetes (*Paralvinella* spp.) on the surfaces of active hydrothermal vent chimneys of Myojin Knoll and Myojin-sho Caldera using a suction sampler (lined with a 30 μm mesh). These annelids are typically distributed in close proximity to vent orifices, where temperatures are the highest among the vent-megafaunal aggregations (Watanabe & Kojima, 2015). At certain chimneys, we took suction samples from patches of *Neoverruca intermedia*, a vent barnacle that occurs within tens of centimetres from the vent orifice. Water temperature measurements were taken with a thermometer at the centre of some of the sampling locations, which showed that the *Neoverruca* patches were cooler than the *Paralvinella* spp. patches by up to 11 °C (Table 1). Since there were no obvious high-density macrofauna aggregations on Bayonnaise Knoll, we collected suction samples from white bacterial mats around the vent orifices of the chimneys. The biogenic substrate, sampling position, water depth and altitude above the bottom of each sampling site are summarized in Table 1.

Upon recovery of the samples on the ship, a small amount of detritus was removed immediately from each detritus sample and frozen without chemical fixation. These samples were used to measure the concentrations of total organic carbon (TOC) and total nitrogen (TN), C/N ratios and stable carbon isotopic compositions ($\delta^{13}C$) to estimate the origins of the organic matter in detritus. Details of the TOC, TN and $\delta^{13}C$ analyses are described by Nomaki *et al.* (2019). The remaining portions of the detritus samples were subdivided into two aliquots using a plankton splitter, and each aliquot was preserved separately in 5% buffered seawater formalin for analysis of the taxonomic composition of meiofauna (used in this study), or 99.5% ethanol for their DNA. Formalin-fixed samples were then stained with rose bengal (final concentration 0.05 g L^{-1}) to help identify live meiofaunal samples.

The details of the process of benthic copepod extraction from the formalin-fixed samples in the laboratory are described in Senokuchi *et al.* (2018). Among the extracted copepod specimens from each sample, we randomly selected adult harpacticoid specimens without serious morphological damage preventing identification, until reaching 50 specimens (or all available specimens when there were <50). The specimens were examined under a compound microscope equipped with differential interference optics. We investigated only adult copepods due to the difficulty associated with morphologically identifying immature individuals. The specimen number in a sample (N = 50) was found to be sufficient for evaluating the overall trend in meiofaunal composition (e.g. Setoguchi *et al.*, 2014). Little is known about the taxonomy of benthic harpacticoids, particularly on deep-sea hydrothermal vents around Japan (e.g. Lee & Huys, 2000; Back *et al.*, 2010); therefore, we did not identify individuals to the species level, only to the family level using a key based on Huys *et al.* (1996), Boxshall & Halsey (2004) and Wells (2007) and recent literature (cf. Walter & Boxshall, 2021).

Statistical analyses

We analysed the entire dataset of harpacticoid composition using a distance-based linear model (DISTLM) and distance-based redundancy analysis (dbRDA), using the Bray–Curtis index as a similarity index (Clarke & Warwick, 2001; Anderson *et al.*,

Table 1. Details of sampling locations, codes, dates, biological and physicochemical parameters

Caldera	Sample ID	Chimney ID	Biogenic Substrate[a]	Cruise ID	Date (d/m/y)	Depth (m)	Latitude	Longitude	Height[b] (m)	Temperature (°C)	Sediment geochemical data[c]
Bayonnaise Knoll	B1a	B1	Bacteria	NT14-06	13/04/2014	778	31°57.363′N	139°44.731′E	0.5	23.7	Exist
	B2a	B2	Bacteria	NT14-06	13/04/2014	760	31°57.332′N	139°44.752′E	1.1	–	Exist
	B3a	B3	Bacteria	NT14-06	13/04/2014	757	31°57.331′N	139°44.765′E	1.2	–	Exist
	B4a	B4	Bacteria	NT14-06	13/04/2014	757	31°57.331′N	139°44.765′E	1	–	–
	B4b		Bacteria	NT14-06	13/04/2014	757	31°57.331′N	139°44.765′E	0.8	–	Exist
	B5a	B5	Bacteria	NT14-06	13/04/2014	742	31°57.319′N	139°44.798′E	0.5	–	Exist
	B6a	B6	Bacteria	NT14-06	15/04/2014	781	31°57.463′N	139°44.726′E	1.5	16.4	Exist
	B6b		Bacteria	NT14-06	15/04/2014	781	31°57.463′N	139°44.726′E	1.7	16.4	Exist
	B7a	B7	Bacteria	NT14-06	15/04/2014	777	31°57.444′N	139°44.744′E	1.1	7.4	Exist
	B8a	B8	Bacteria	NT14-06	16/04/2014	774	31°57.432′N	139°44.736′E	1.3	34.2	Exist
	B8b		Bacteria	NT14-06	16/04/2014	774	31°57.432′N	139°44.736′E	1.3	34.2	Exist
	B9a	B9	Bacteria	NT14-06	16/04/2014	772	31°57.424N	139°44.744′E	1.3	150.9	Exist
	B10a	B10	Bacteria	NT14-06	16/04/2014	772	31°57.424N	139°44.744′E	1.3	85.8	Exist
Myojin-sho Caldera	S1a	S1	Paralvinella	NT12-10	25/04/2012	809	31°53.038′N	139°58.210′E	1.3	–	Exist
	S2a	S2	Paralvinella	NT13-09	24/04/2013	795	31°53.042′N	139°58.220′E	3.2	–	Exist
	S2b		Paralvinella	NT13-09	24/04/2013	795	31°53.042′N	139°58.220′E	3.4	–	Exist
	S2e		Paralvinella	NT13-09	24/04/2013	795	31°53.042′N	139°58.220′E	3.4	–	Exist
	S3a	S3	Paralvinella	NT14-06	18/04/2014	850	31°53.028′N	139°58.170′E	9.4	13.4	Exist
	S3b		Neoverruca	NT14-06	18/04/2014	850	31°53.028′N	139°58.170′E	10.7	6.5	Exist
	S4a	S4	Paralvinella	NT14-06	18/04/2014	817	31°53.039′N	139°58.201′E	1.6	9.6	Exist
	S4b		Neoverruca	NT14-06	18/04/2014	817	31°53.039′N	139°58.201′E	1.5	7	Exist
	S5a	S5	Paralvinella	NT14-06	18/04/2014	791	31°53.051′N	139°58.212′E	7.7	17.9	Exist
	S5b		Neoverruca	NT14-06	18/04/2014	791	31°53.051′N	139°58.212′E	5.6	6.5	Exist

(Continued)

Table 1. (*Continued.*)

Caldera	Sample ID	Chimney ID	Biogenic Substrate[a]	Cruise ID	Date (d/m/y)	Depth (m)	Latitude	Longitude	Height[b] (m)	Temperature (°C)	Sediment geochemical data[c]
Myojin Knoll	K1a	K1	*Paralvinella*	NT12-10	29/04/2012	1321	32°06.286′N	139°52.096′E	0.7	–	Exist
	K1b		*Neoverruca*	NT12-10	29/04/2012	1321	32°06.286′N	139°52.096′E	0.7	–	Exist
	K2a	K2	*Paralvinella*	NT12-10	29/04/2012	1249	32°06.214′N	139°52.053′E	12.7	–	Exist
	K2b		*Neoverruca*	NT12-10	29/04/2012	1249	32°06.214′N	139°52.053′E	12.7	–	–
	K2c		*Paralvinella*	NT13-09	26/04/2013	1251	32°06.222′N	139°52.047′E	15.6	–	Exist
	K2d		*Paralvinella*	NT13-09	26/04/2013	1251	32°06.222′N	139°52.047′E	9.3	–	Exist
	K3a	K3	*Paralvinella*	NT13-09	28/04/2013	1268	32°06.215′N	139°52.053′E	2.7	–	Exist
	K4a	K4	*Paralvinella*	NT13-09	28/04/2013	1250	32°06.205′N	139°52.052′E	4	–	Exist
	K5a	K5	*Paralvinella*	NT13-09	26/04/2013	1307	32°06.284′N	139°52.092′E	1.1	–	Exist

[a]Bacteria, bacterial mat; Paralvinella, Paralvinella patch; Neoverruca, Neoverruca patch. [b]Height above bottom recorded by the ROV altimeter during fixed position sampling. [c]Data on parameters of detritus organic matter are cited from Nomaki et al. (2019).

2008). Suction samples from the chimney surface were generally taken from areas of $\sim 20 \times 30\ cm^2$ on common biogenic substrata (e.g. patches of *Paralvinella* spp.), but we encountered difficulties in precisely tracing the sampling areas from video and photographs, which were usually captured at inappropriate angles to identify the exact sampling points. Thus, statistical analyses were performed based on standardized values of family composition (percentage of each family in total identified specimens) for each sample, as opposed to their actual density (ind. cm^{-2}). We used PRIMER7 software with the add-on package PERMANOVA+ (PRIMER-E Ltd, Plymouth, UK) for these analyses.

DISTLM was used to determine the best-fit models and partition variance in the response variables (harpacticoid compositions) to assign proportional effects to the measured environmental factors (Anderson et al., 2008).

The environmental factors TOC concentration in detritus, C/N ratio (weight/weight), $\delta^{13}C$ values, water depth and the height from the chimney base where the sample was collected (altitude) were considered in the analysis. The $\delta^{13}C$ values and C/N of organic matter in the detritus are indicators of the relative contributions of different carbon sources. In our previous study, the $\delta^{13}C$ values of vent chimney detritus ranged from −24 to −11%, a range between typical photosynthetic organic carbon and chemoautotrophic organic carbon (Nomaki *et al.*, 2019). The C/N ratios of chemoautotrophic organic matter in detritus tend to be lower (Limén *et al.*, 2007). In addition to these geochemical factors, we also considered water depth and altitude as potential factors controlling copepod composition. Bathymetric changes in community composition have been reported among benthic harpacticoids at the (non-vent) deep-sea bottom (e.g. Shimanaga *et al.*, 2019). The mean depths at sampling sites in Bayonnaise Knoll, Myojin-sho Caldera and Myojin Knoll were 768, 811 and 1274 m, respectively (cf. Table 1). Although we could not include temperature in our overall multivariate analyses due to the limited *in situ* temperature data (N = 14 out of 32), preliminary DISTLMs based on a limited temperature dataset did not select the temperature as a significant parameter, suggesting its low association with spatial heterogeneity in harpacticoid composition at least at family level.

Benthic harpacticoids have large variations in their body shapes based on their lifestyles; some of them are large and have free-swimming abilities (Hicks & Coull, 1983). Around the hydrothermal vents, many meiofauna species including harpacticoids are generalists that can live on active vents and non-vent seafloor, and they were suggested to populate new vent sites by crawling or swimming from their old habitats (Gollner *et al.*, 2020). Although the effects of chimney height (altitude of the sampling spot from the base of the chimney) on meiofaunal composition at hydrothermal vent fields are still unknown, this may affect the differences in vertical distribution on chimneys between the harpacticoids with different swimming abilities.

While we used standardized values of harpacticoid families for each sample before calculating similarities between samples, the values of those environmental factors were not transformed, as PERMANOVA+ automatically normalizes each environmental factor when running DISTLM (Anderson *et al.*, 2008). The forward selection procedure was used to determine the best combination of predictor variables to explain variation in harpacticoid composition data and to partition the variation explained by the selected predictor variables based on the selection criterion (AIC, in this study). The dbRDA was used to ordinate the fitted values from the models selected by DISTLM (Anderson *et al.*, 2008).
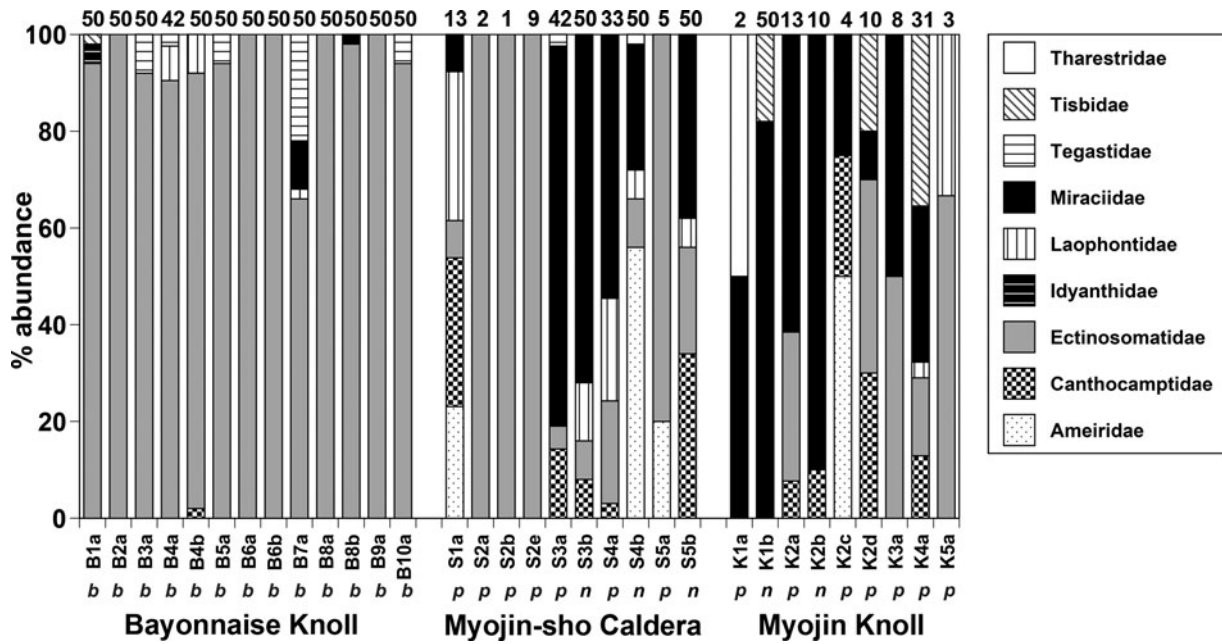
Fig. 2. Spatial differences in harpacticoid family composition among samples from active chimneys. The numbers above each bar denote the number of specimens obtained on each sample. *b*, bacterial mats; *p*, patches of *Paralvinella* spp.; *n*, patches of *Neoverruca intermedia*.

Results

Among 1028 adults investigated, nine harpacticoid families were recognized (Figure 2). Ectinosomatidae was the most abundant family at the bacterial mats on the chimneys in Bayonnaise Knoll (Figure 2), comprising 94% of the total identified specimens collected from the knoll (Figure 3). Their relative abundances were about 25% among the total specimens collected from the patches of *Paralvinella* polychaetes on the chimneys in both Myojin-sho Caldera and Myojin Knoll; although, in some patches where only a few harpacticoid specimens were obtained (e.g. S2a, b in Figure 2), all of the samples were from the Ectinosomatidae family. Ectinosomatids were fewer in the community at the patches of *Neoverruca* barnacles (13% in Myojin-sho, 0% in Myojin Knoll, Figure 3). In contrast, Miraciidae comprised only 1% of the total adult harpacticoids from Bayonnaise Knoll, whereas its frequency increased on the chimneys in Myojin-sho Caldera ($\sim$50% at both macrofaunal patches), and in the Myojin Knoll (35% in *Paralvinella* patches, 83% in *Neoverruca*, Figure 3). The χ^2 test based on the pooled data, ignoring the differences in biological patches, revealed that the frequencies of families were significantly different among the knolls ($P < 0.01$). Other χ^2 tests also detected significant differences at the 1% level in the frequencies between *Paralvinella* and *Neoverruca* patches in both Myojin-sho Caldera and Myojin Knoll when the consideration was restricted to separate samples from each sea knoll.

Based on samples for which we had data on harpacticoid family level compositions and those of environmental parameters (detritus TOC concentration, δ^{13}C values, C/N ratios, water depth, and height of sampling positions on the chimney walls, Table 1 and Figure 4), DISTLM showed significant associations between four out of five investigated environment factors and spatial differences in harpacticoid composition separately, but δ^{13}C of the detritus of the habitat (i.e. potential food sources) did not reveal a significant correlation by itself (marginal tests in Table 2). On the other hand, the forward selection processes in DISTLM selected all investigated parameters, including δ^{13}C of the detritus, as factors explaining 65.5% of the total spatial variation in composition difference among samples (Table 2). The
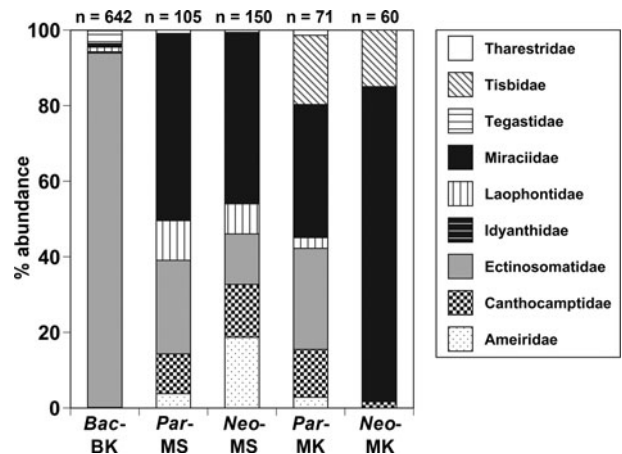

Fig. 3. Frequencies of harpacticoid families in the pooled specimens obtained from different biogenic substrata on chimneys in the three calderas. n, total specimen number for each category; *Bac*-BK, bacterial mats on chimneys on Bayonnaise Knoll; *Par*-MS and *Neo*-MS, patches of *Paralvinella* spp. and *Neoverruca intermedia*, respectively, on chimneys in Myojin-sho Caldera; *Par*-MK and *Neo*-MK, patches of *Paralvinella* spp. and *Neoverruca intermedia*, respectively, on chimneys in Myojin Knoll.

spatial heterogeneities of water depth were the most important factors explaining 22% of the total variation in composition difference among samples, followed by TOC (12%) and the differences in the height of the sampling position (12%). The contributions of δ^{13}C and C/N of the detritus of the habitat (i.e. potential food sources) were smaller ($\sim$6%).

The dbRDA based on the DIRSTLM results showed that the spatial heterogeneities of water depth and TOC contributed mainly to the difference in harpacticoid composition between the knolls (Figure 5A), as the proportion of Miraciidae (expressed by the sizes of black segments of bubble plots in Figure 5B) were positively correlated with these factors, and were greater on Myojin-sho and Myojin Knolls. The relative abundances of Ectinosomatidae (grey segments of bubble plots in Figure 5B) were negatively correlated with these factors and showed a tendency to increase in Bayonnaise Knoll. The values of δ^{13}C and
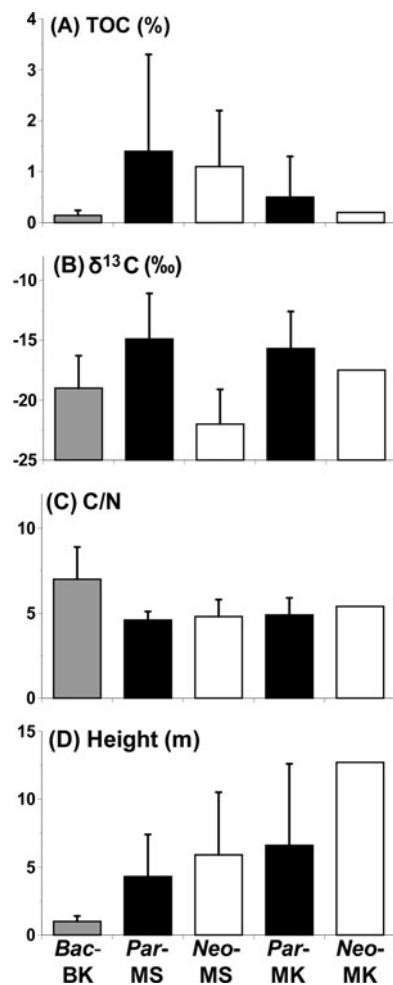
Fig. 4. Spatial changes in (A) concentration of total organic carbon (TOC), (B) stable carbon isotopic compositions ($\delta^{13}C$), and (C) Total organic carbon/total nitrogen ratio (C/N), (D) height of the sampling point above the seafloor. Bars and error bars denote averages and standard deviations (SDs), respectively. *Bac*-BK, bacterial mats on chimneys in Bayonnaise Knoll; *Par*-MS and *Neo*-MS, patches of *Paralvinella* spp. and *Neoverruca intermedia*, respectively, on chimneys in Myojin-sho Caldera; *Par*-MK and *Neo*-MK, patches of *Paralvinella* spp. and *Neoverruca intermedia*, respectively, on chimneys on Myojin Knoll.

C/N had weak positive associations with the higher frequencies of the family.

Discussion

Previous studies have shown that the lower diversity of meiofauna, including copepods, at deep-sea hydrothermal vent sites with high hydrothermal influence, suggests that environmental conditions around vents affect meiofaunal taxa more negatively than larger macrofauna (Tsurumi et al., 2003; Zekely et al., 2006b; Gollner et al., 2010a, 2015a). While most of the described copepod species from the deep-sea hydrothermal vents belong to the family Dirivultidae (order Siphonostomatoida), which has been reported exclusively in those ecosystems, other copepod families of the Harpacticoida and Cyclopoida orders from hydrothermal vents have been previously identified in shallow waters (Zeppilli et al., 2018).

The present study showed simple and similar compositions at the family level of meiofaunal-sized harpacticoids collected from active chimneys on each investigated sea knoll. Especially at the bacterial mats on the chimneys in Bayonnaise Knoll, harpacticoid communities were close to being monopolized by Ectinosomatidae (>90%). In contrast, the family level composition

of harpacticoids at vent sites was significantly different between the biological substrata, but also between the knolls, suggesting caldera walls function as barriers, as expected. The frequency of Ectinosomatidae was lower on average on the chimneys in both Myojin-sho Caldera and Myojin Knoll, where Miraciidae contributed more to the harpacticoid composition, especially at *Neoverruca* patches.

The copepod family Dirivultidae (Siphonostomatoida), a typical vent copepod group, has planktonic nauplii and/or copepodid stages and strong swimming abilities (Ivanenko, 1998; Gollner et al., 2015a), and members of this family migrate either as larvae and/or free-swimming adults from an active vent source to other active vent sites (cf. Gollner et al., 2020). In contrast to the high abundance of dirivultids, very low frequencies of benthic harpacticoids occurred in the water column above the same vent habitats (Gollner et al., 2015b), suggesting their lower locomotive abilities around the vent habitats. The swimming ability of some harpacticoids, however, may be sufficient to migrate occasionally between neighbouring chimneys. On the continental slope near central California, Thistle et al. (2007) showed that some deep-sea harpacticoid species demonstrated emergence behaviour, temporary excursions into the water column above the sea bottom, and the majority of these emergent species belonged to Ectinosomatidae, suggesting that deep-sea species of this family are strong swimmers similar to their relatives in shallow waters. Although the identification at lower taxonomic levels is still ongoing for our harpacticoid specimens, preliminary surveys suggest that ectinosomatids on the chimneys in Bayonnaise Knoll are composed of *Ectinosoma* spp., which also appeared to be distributed in the sediment on the non-venting seafloor at the bases of those chimneys. Further studies at genus and species levels on harpacticoid compositions on the surfaces of venting chimneys and in the sediment of their neighbouring seafloor would help clarify the processes of the foundation and maintenance of populations of ectinosomatids at our investigated vent sites.

After a major volcanic eruption in 2005/2006 buried faunal communities over a large area of the vent field in the 9°N East Pacific Rise (EPR), harpacticoid copepods such as *Amphiascus* aff. *varians* (Miraciidae) contributed as meiofaunal colonizers of new active vent sites (Gollner et al., 2020). These meiofaunal harpacticoids would have reached those new vent sites predominantly via migration from local refuge areas that were not disturbed by the eruption (Gollner et al., 2020), suggesting that the Miraciidae species observed at those vent sites, as well as our sites, have stronger swimming abilities than other harpacticoids.

There were general bathymetric trends in harpacticoid community composition on the (non-vent) deep-sea bottom from the upper bathyal to abyssal depths (400–5800 m) along the Pacific side of the Japanese island arc, where Ectinosomatidae was the most abundant family at upper bathyal depth, but was consistently decreased with increasing water depth (Shimanaga et al., 2019). This trend could at least partly explain the observation of the highest frequencies of Ectinosomatidae on vent chimneys in the caldera of Bayonnaise Knoll, which has the shallowest depths (770 m on average) among the three knolls investigated in this study. In the foundation and maintenance of communities of non-vent-endemic meiofauna, including most of the harpacticoids, at deep-sea vent fields, the invasion from adjacent non-vent areas would have been more important than the migration from the other isolated hydrothermal vents due to the lack of a planktonic life stage (cf. Vanreusel et al., 1997). It is noteworthy that the DISTLM identified water depth as the most significant factor explaining the spatial change in harpacticoid composition at vent sites in this study. To confirm this proposal, further information on harpacticoid composition on the non-vent seafloor surrounding the vent chimneys investigated in this study will be essential.

Table 2. Distance-based linear model (DISTLM) analyses of harpacticoid composition

Marginal tests				
Variables[a]	Pseudo-*F*	*P*	Var. (%)[b]	
TOC	6.7	**0.001**	19.4	
δ^{13}C	0.2	0.920	0.6	
C/N	5.7	**0.005**	16.9	
height	5.8	**0.007**	17.2	
depth	8.1	**0.002**	22.3	
Sequential tests (forward selection procedure)				
Variables[a]	Pseudo-F	*P*	Var. (%)[b]	Cumulative (%)[c]
+depth	8.1	**0.0023**	22.3	22.3
+TOC	5.1	**0.0120**	12.4	34.8
+height	5.9	**0.0030**	12.0	46.8
+δ^{13}C	3.3	**0.0252**	6.2	53.0
+C/N	3.3	**0.0241**	5.7	58.8

[a]Variables tested as predictors in the analyses. Significant *P*-values are shown in bold with under lines. δ^{13}C denotes those of organic matter in detritus. [b]Percentage of total variation explained by the factor. [c]Cumulative percentage explained by the added factors.

The concentration of TOC in detritus was selected as the second factor explaining the harpacticoid distribution, and Ectinosomatidae dominated at the sites where lower TOC was observed in Bayonnaise Knoll. The processes by which a lower TOC drives a higher frequency of the family are unclear based on current available data. The vent chimneys in Bayonnaise Knoll were generally smaller than those in the other two knolls (Figure 4b) and without apparent patches of large sessile mega- and macrofauna on their surfaces, suggesting that the total amount of organic input was too small to sustain the larger fauna. This reduction of food availability may affect both macro-fauna and meiofaunal harpacticoids.

In the present study, δ^{13}C and C/N of organic matter in the detritus, indicators of relative contributions of different carbon sources, showed low affinities with the spatial difference in family-level harpacticoid composition, suggesting that chemoautotrophic food availability is not the main factor controlling harpacticoid distribution on the active chimneys in the investigated sea knolls. We have not yet measured and compared δ^{13}C values of body tissues between different harpacticoid taxa. Interestingly, however, the preliminary study showed the mixed samples of several tens of copepods other than dirivultids (mainly harpacticoids) in this study area had lower δ^{13}C values than dirivultids, suggesting that they utilized a mixture of photosynthesis- and chemosynthesis-derived carbon resources (Nomaki *et al.*, 2019). This may reinforce a possibility that harpacticoids at the investigated vents do not feed exclusively on chemoautotrophic food, but also adopt marine snows from sea surface onto chimneys as a total harpacticoid community. Ectinosomatids also dominated in harpacticoid specimens from some patches of *Paralvinella*, where most benthic copepods found were vent-endemic dirivul-tids (Senokuchi *et al.*, 2018), and smaller numbers of harpacti-coids were obtained (Figure 2). Since dbRDA suggested weak but positive associations between δ^{13}C and C/N and the frequency of Ectinosomatidae, the species of the family may be affected by the gradient of chemosynthesis-derived carbon availability more strongly than the other harpacticoids observed in the study vent sites.

A potential impediment to the present study is that no com-mon biological substratum was collected from all investigated

vent areas in the three knolls. For example, in Bayonnaise Knoll, the shallowest among the three knolls, there were only bac-terial mats with lower TOC concentrations in detritus on shorter chimneys than those of the other knolls. Based on these available sample sets, it is possible that the effects of differences in these substrata (and their foundation macrofauna species themselves) and environmental factors would be correlated with each other and subsequently affect the observed harpacticoid distribution.

The comparisons between our results and previous studies suggest that harpacticoid composition at deep-sea vents in the various provinces is considerably different from each other, even at the family level.

On the Juan de Fuca Ridge in the eastern Pacific (45–48°N), higher frequencies of harpacticoids than dirivultids are observed on the basalt and sulphide habitats with lower venting flow, where most harpacticoids were of the family Miraciidae (Tsurumi *et al.*, 2003). Particularly on 'blue mats', which were formed by colonial folliculinid ciliates and occupied as much as 70% of the basaltic substratum at the hydrothermal vent sites on the Juan de Fuca and the adjacent Explorer Ridges, most ben-thic copepods were composed of one undescribed species of the family (*Amphiascus*; Kouris *et al.*, 2010). As mentioned above, a species of *Amphiascus* (Miraciidae), distributed in both vent and non-vent fields, also contributed as meiofaunal colonizers of new active vent sites (2500 m) in the 9°N EPR (Gollner *et al.*, 2015b, 2020).

In the meiofaunal communities associated with *Bathymodiolus* mussel aggregations in the Mid-Atlantic Ridge (MAR, 11°N) and EPR (23°N), most copepod species were vent endemic dirivultids, and harpacticoid copepods contributed only a minor percentage to the total permanent meiofauna, which were com-posed of only two families, Ectinosomatidae and Laophontidae, with higher frequencies of the former in both areas (on average 70–90% of harpacticoids, Zekely *et al.*, 2006b).

Colonization experiments deployed at the Lucky Strike vent field on the MAR (37°N, 1698 m) also suggested that environ-mental differences affect copepod composition (Ivanenko *et al.*, 2011). At the base of a black smoker, the harpacticoids of Ectinosomatidae, Ameiridae or Argestidae were the most abun-dant (58–80% of total benthic copepods), whereas the frequencies
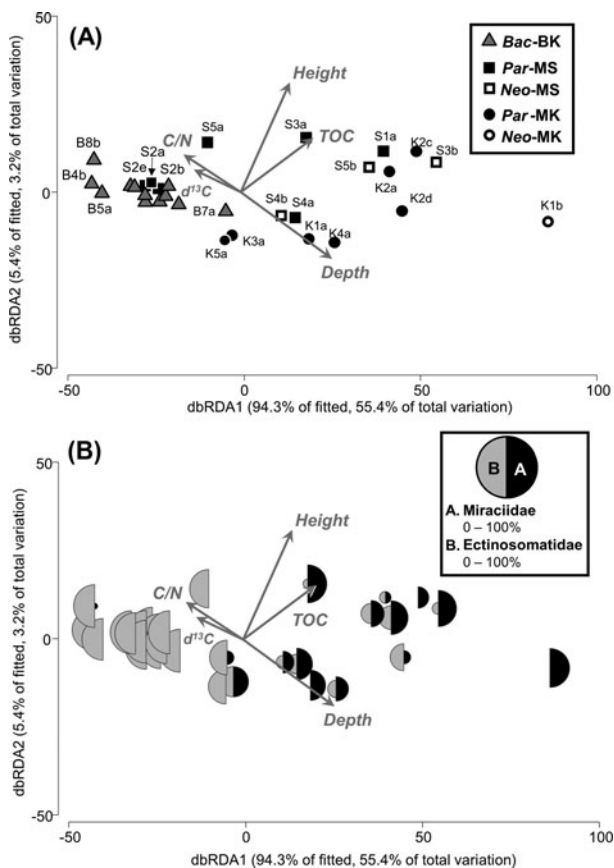
Fig. 5. (A) Distance-based redundancy analysis (dbRDA) of the harpacticoid family-level composition dataset according to distance-based linear modelling (DISTLM) with selected environment factors. The percentages of variation in the fitted model and in the total variation in harpacticoid composition explained by each of the dbRDA axes are indicated. The directions and lengths of vector overlays denote the directions and strengths of the relationships between the dbRDA axes and the environmental factors, respectively. Different symbols refer to different habitats where sampling was conducted. *Bac*-BK, bacterial mats on chimneys in Bayonnaise Knoll; *Par*-MS and *Neo*-MS, patches of *Paralvinella* spp. and *Neoverruca intermedia*, respectively, on chimneys in Myojin-sho Caldera; *Par*-MK and *Neo*-MK, patches of *Paralvinella* spp. and *Neoverruca intermedia*, respectively, on chimneys on Myojin Knoll. Particular sample codes are arrayed next to the symbols. (B) Segmented bubble plot for the main copepod taxa (A, Miraciidae; B, Ectinosomatidae) on the ordination plotted in (A). Differences in size between segmented bubbles indicate relative abundances of the taxa (0–100%).

of Tisbidae (*Tisbe* spp.) harpacticoids were higher (>80% maximum) on *Bathymodiolus* mussel assemblages, together with dirivultids, cyclopoids and the harpacticoid species of Tegastidae (*Smacigastes micheli*).

A recent colonization experiment held in Lucky Strike vent field confirmed that the gradient of venting fluid input, rather than the difference in the substrata used for the experiment, mainly influenced the copepod composition colonizing the substrata; *S. micheli* and *Tisbe* sp. contributed to 36–74% of the average similarity among the samples from the most active area and from another site characterized by the presence of *Bathymodiolus* mussels and microbial mats with intermediate fluid inputs (Plum *et al.*, 2017). Very recently, at the ABE vent site (2142 m) in the Lau Basin, the south-western Pacific, Lorenzo *et al.* (2021) reported that *Amphiascus* aff. *variance* were the most abundant harpacticoids (3–38%), followed by a species of Tisbidae (4–16%) on the *Bathymodiolus* communities, but very few harpacticoids were observed from those of *Alviniconcha* and *Ifremeria* snails correlated with higher temperature and hydrogen sulphide concentrations. Those recent studies suggest that physicochemical conditions are important drivers of copepod colonization patterns at hydrothermal vents.

Although we could not include temperature in our overall multivariate analyses due to the limited *in situ* temperature data (Table 1), our previous study showed a higher association of $\delta^{13}C$ values of organic matter in detritus with the copepod distribution at the order level (Senokuchi *et al.*, 2018). This showed that $\delta^{13}C$ of detritus, mainly controlled by the contribution of organic matters produced by the chemoautotrophic prokaryotes, can explain spatial differences in copepod compositions, and can be a parameter for environmental gradients around vents, considering that chemosynthetic production is high under hot and sulphide-rich conditions. Thus, the low affinity between $\delta^{13}C$ and harpacticoid composition observed in the present study also may suggest that the physicochemical gradients around vents are not a significant driver of the spatial differences in harpacticoid communities in the study area.

Another possibility is that the present sample set did not cover the whole harpacticoid community on the vent sites in our study area, which may lead to the observed low relations of harpacticoid composition with chemosynthetic gradients; Tisbidae and Tegastidae showed low frequencies in our available samples. Since high frequencies of Tisbidae and/or Tegastidae have been reported in *Bathymodiolus* mussel assemblages at the vent sites in different areas (e.g. Ivanenko *et al.*, 2012; Plum *et al.*, 2017; Lorenzo *et al.*, 2021), the harpacticoid samples taken from the bed of *Bathymodiolus septemdierum*, a species of *Bathymodiolus* mussels observed at the vents in Myojin Knoll and the other knolls on the Izu-Ogasawara Arc (Watanabe *et al.*, 2010), are required for the next stage.

In summary, we detected significant differences in harpacticoid composition between the vent sites of the three knolls, even at the family level. However, high similarities in the composition were observed between the same biological substrates on different chimneys in each knoll, suggesting connectivity between populations on adjacent vent chimneys by the dominant taxa (Ectinosomatidae or Miraciidae), probably with strong swimming abilities as their relatives have shown in other habitats. While high associations between harpacticoid composition, water depth and TOC concentration were detected, the availability of vent chemoautotrophic food did not seem to be the main factor controlling the harpacticoid composition around the vents investigated in this study.

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