



## Benthic community structure on two peaks of an erupting seamount: Northwest Rota-1 Volcano, Mariana Arc, western Pacific

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**Abstract:** This study examined structural features of a vent ecosystem subject to perturbation by repeated underwater eruptive activity on NW Rota-1 Volcano in the Mariana Arc. Results provide insight into how chronic disturbance regimes shape vent ecosystems. A photosynthetically-based, deep-sea sessile community found on an inactive peak of NW Rota-1 was completely absent from the volcanically and hydrothermally active peak, even away from the areas of venting. A slightly more complex community and food web occurred where fluids were venting through cemented lavas (versus volcanoclastic sand), underlining the importance of substratum stability to the vent fauna. Meiofauna abundance and sediment organic matter content were much lower at these vents, compared to the nearby inactive peak, pointing to the importance of organic matter accumulation for the establishment of meiofaunal communities on the volcanic substratum. Evidence for food partitioning and multiple organic matter sources indicates that these latter are fundamental features of even chronically disturbed vent communities.

**Keywords:** Hydrothermal vent • Benthic community • Disturbance • Food Web • Meiofauna • Food partitioning • Stable isotopes

### Introduction

The variable and severe habitat conditions that characterize hydrothermal vent environments provide many opportunities to explore how benthic species and communities respond to their physical environment. Early ecological studies documented species distribution along environmental gradients away from vent openings and later recognized more complex patterns of species distribution in heterogeneous habitats such as sulfide edifices (Hessler & Smith, 1983; Sarrazin et al., 1999). Many of these distribution patterns can be explained in terms of physiological responses to dissolved chemical concentrations or chemical speciation (Luther et al., 2001) and habitat selection by individual species (Bates et al., 2005). Physical disturbance can also be a structuring factor in vent communities (Shank et al., 1998; Sarrazin et al., 1999). Time series studies in habitats on rapidly growing sulfide edifices and following seafloor eruptions have permitted researchers to document the *de novo* colonization process (Tunnicliffe et al., 1997; Shank et al., 1998), food web assembly (Shank et al., 1998;

1983; Sarrazin et al., 1999). Many of these distribution patterns can be explained in terms of physiological responses to dissolved chemical concentrations or chemical speciation (Luther et al., 2001) and habitat selection by individual species (Bates et al., 2005). Physical disturbance can also be a structuring factor in vent communities (Shank et al., 1998; Sarrazin et al., 1999). Time series studies in habitats on rapidly growing sulfide edifices and following seafloor eruptions have permitted researchers to document the *de novo* colonization process (Tunnicliffe et al., 1997; Shank et al., 1998), food web assembly (Shank et al., 1998;

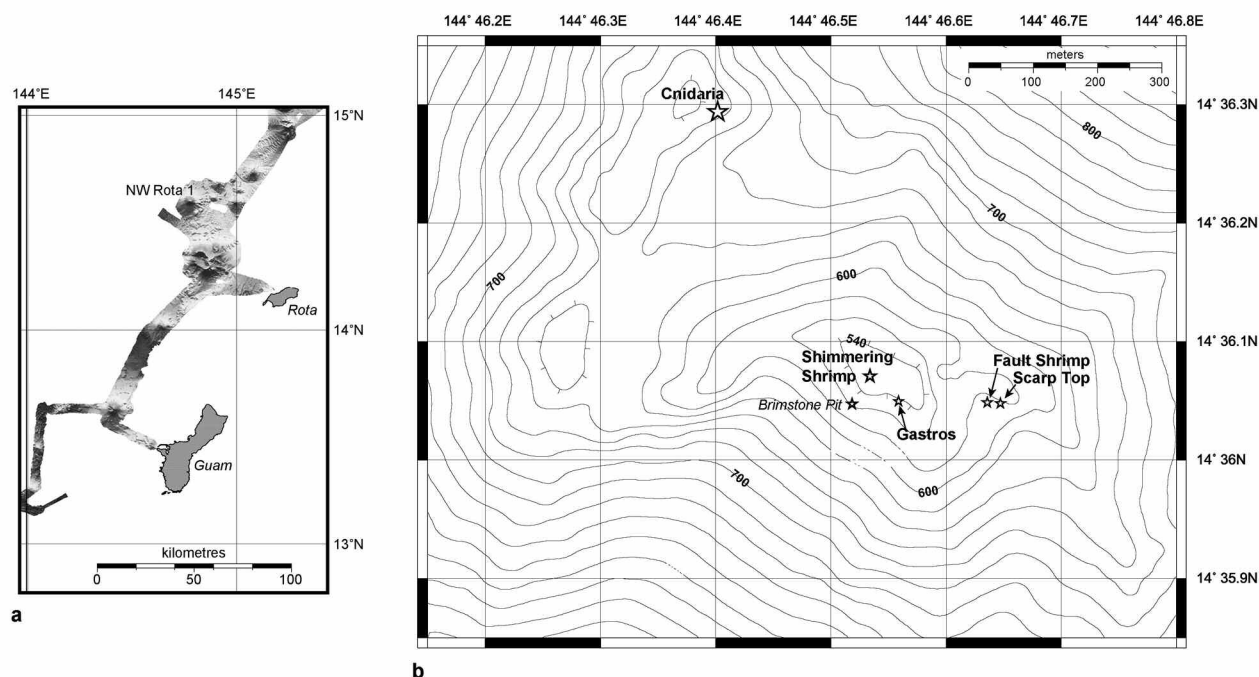
Levesque et al., 2003 & 2006) and to develop models of community responses to perturbations and habitat evolution (Tsurumi & Tunnicliffe, 2001). The present study considered structural features of a vent ecosystem subject to chronic perturbation by repeated underwater eruptive activity. We examined macrofaunal and meiofaunal community composition and food web characteristics at vents on a seafloor volcano in the Mariana Volcanic Arc. Samples from an adjacent inactive peak of the same volcano were included for comparison. Results provide insight into which elements of vent ecosystems are best adapted to chronic disturbance regimes.

The volcanic arcs of the western Pacific Ocean host about 600 individual submarine volcanoes, most of which have not been surveyed for hydrothermal activity. Those that have been investigated encompass a remarkable range of hydrothermal and volcanic conditions (Ishibashi & Urabe, 1995; Embley et al., 2004). Exploratory ROV submersible dives in 2004 on an active submarine volcano in the Mariana Arc provided an opportunity to investigate the structure of vent communities in an unstable volcanic-hydrothermal vent system. We report here on observations and samples from NW Rota-1 Volcano, which is presently subject to frequent eruptive activity (Embley et al., 2006).

## Materials and Methods

In March/April 2004 the R/V Thomas G. Thompson and the remotely-operated vehicle (ROV) ROPOS were used to sample fauna and particulate organic matter from the NW Rota-1 volcano. This volcano, located at 14°36.0'N, 144°46.5' E, 60 km northwest of Rota Island in the Mariana Volcanic Arc (Fig. 1a), has a central peak (530 m depth) with sustained volcanic and hydrothermal activity and an inactive side peak at 600 m depth (Fig. 1b). Eruptive activity was concentrated in a 15 m-diameter crater (Brimstone Pit, Fig. 1b) on the south flank of the central peak. Dense clouds of molten sulphur were constrained to the Pit but volcanic ejecta carpeted the entire peak, forming 'angle-of-repose' slopes around the summit. Multiple turbid layers containing volcanic ash were detected in the water column from 700 m down to at least 1900 m (Embley et al., 2006). Diffuse hydrothermal venting occurred around the Pit and elsewhere on the central peak, where clear fluids up to 65°C were venting through bare lavas and coarse volcanoclastic sand. Neither hydrothermal activity nor evidence of recent volcanism was observed on the side peak of the volcano, 500 m to the northwest (Fig. 1b).

Four sites were sampled on the active peak, together with one site on the hydrothermally inactive peak (Fig. 1b).



**Figure 1. a.** Location of Northwest Rota-1 volcano in the Mariana Arc, near the islands of Rota and Guam. **b.** Bathymetric map showing locations of sampling sites on the summit of Northwest Rota 1 volcano.

**Figure 1. a.** Localisation du volcan Rota-1 nord-ouest dans l'Arc des Mariannes, près des Iles de Rota et Guam. **b.** Carte de la bathymétrie montrant la localisation des sites d'échantillonnage sur le sommet du volcan Rota-1 nord-ouest.

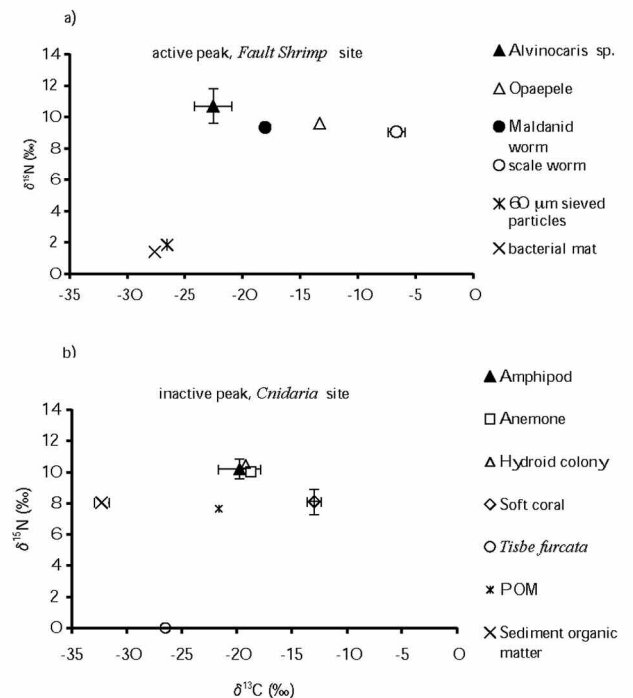
Fauna and particulate organic matter were collected at all sites using the ROPOS suction sampler. Samples were collected into 2 L acrylic jars and the suction hose was flushed with bottom seawater between samples to minimize cross contamination. On board the ship, samples were sorted and frozen at  $-80^{\circ}\text{C}$  until analysis. In addition, a single, near-bottom (40 m altitude) suspended particulate organic matter (POM) sample was collected during a transit from the active to the inactive peak, using a modified McLane pump system mounted on ROPOS. POM was concentrated onto a pre-weighed, pre-combusted 142 mm diameter GF/F filter by pumping 1250 L of ambient seawater at 5 litres per minute through an intake on the forward frame of the submersible. Upon recovery, the filter was immediately wrapped in aluminum foil and frozen at  $-80^{\circ}\text{C}$ .

Specimens were identified to the lowest possible taxon and enumerated under a microscope. Stable carbon and nitrogen analysis was performed on individual macrobenthic species. For meiofaunal organisms, such as harpacticoid copepods, up to 200 individuals of the same species were pooled together to obtain sufficient biomass for analysis. Some samples were too small to yield dual isotope signatures, and for these we report only the carbon isotopic ratio. All samples were acidified, dried and analyzed using a Micromass Isoprime isotope ratio mass spectrometer, in line with a Carlo Erba C/N element analyzer. Stable isotopic compositions are reported relative to Vienna Pee-Dee Belemnite and atmospheric nitrogen.

## Results

Benthic communities on the active peak were relatively simple and were composed mainly of mobile vent endemic organisms. Sessile deep-sea organisms were not apparent on any rocks that were outcropping through the volcanic sediment. The most abundant animals were two alvinocarid shrimp species: *Opaepele loihi* Williams & Dobbs, 1995 and *Alvinocaris* sp. nov. (Table 1). Low abundances of the crab *Austinograea yunohana* Takeda et al., 2000 occurred with the shrimp. The only other visible species present on the active peak were the slit limpet *Shinkailepas* (sp. nov. A. Warén, pers. comm.), the polynoid polychaete, *Branchinotogluma* sp., and three maldanid polychaetes. Sediments from Fault Shrimp site contained low abundances of copepods (Table 1) and had the highest organic matter content ( $C_{\text{org}} = 0.21\%$  dry weight). In contrast, the coarse volcanoclastic sediments from Gastros, Scarp Top and Shimmering Shrimp sites had less than 0.10% organic matter content and contained no meiofauna.

None of the macrobenthic species on the active peak was found at the Cnidaria site on the inactive peak. One meio-



**Figure 2.** Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic signatures of invertebrates and particulate and suspended organic matter at the **a)** active peak, and **b)** inactive peak. Error bars represent standard error.

**Figure 2.** Signatures isotopiques du carbone ( $\delta^{13}\text{C}$ ) et de l'azote ( $\delta^{15}\text{N}$ ) stables des invertébrés et de la matière organique en suspension sur **a)** le pic actif et **b)** le pic inactif. Les barres d'erreur représentent l'erreur standard.

faunal species, a harpacticoid copepod, *Tisbe furcata* Baird, 1837, was present at both the inactive and active sites but was more abundant at the inactive site. The macrobenthic community on the inactive peak was visually dominated by anemones, soft corals, hydroids, amphipods, isopods and polychaetes (Table 1). Many more megafaunal species were seen here including a variety of fishes, crabs, and jellyfish, although sampling was not possible. Sediments at the Cnidaria site had the highest organic matter content ( $C_{\text{org}} = 0.30\%$  dry weight) and the most abundant and diverse meiofauna, dominated by harpacticoid copepods and ostracods (Table 1).

While all of these communities had relatively few species, there are some discernable trophic patterns. The stable carbon isotope data for the 4 sampled vent sites show a trend toward diversification of food sources and partitioning by the fauna, as the number of species in the community increased (Table 2 and Fig. 2). Faunal carbon isotopic signatures had the broadest range at the *Fault Shrimp* site ( $-6.6$  to  $-22.5\text{‰}$ ; Fig. 2), where five faunal

**Table 1.** Species list from collections at active and inactive peaks of NW Rota-1 volcano; on the actively erupting peak animals occurred only at sites of hydrothermal venting. Relative abundance is indicated: xxx = very abundant, xx = abundant; x = present.

**Tableau 1.** Liste des espèces récoltées sur les pics actif et inactif du volcan Rota-1 nord-ouest ; sur le pic en éruption, les animaux sont seulement présents au niveau des sources hydrothermales. L'abondance relative est indiquée : xxx = très abondant, xx = abondant, x = présent.

Taxon		Active peak	Inactive peak
<b>Crustacea</b>			
<i>Opaepele loihi</i>	Alvinocaridae	xxx	
<i>Alvinocaris</i> n.sp.	Alvinocaridae	xxx	
<i>Austinograea yunohana</i>	Bythograeidae	xx	
<b>Amphipoda</b>			
sp. unk.			xxx
<b>Isopoda</b>			
sp. unk.			x
<b>Copepoda</b>			
sp. 1	Siphonostomatoida	x	
sp. 2	Siphonostomatoida	x	
<i>Tisbe furcata</i>	Harpacticoida	x	xxx
<i>Halectinosoma angulifrons</i>	Harpacticoida		x
<i>Amphiascus minutus</i>	Harpacticoida		x
<i>Ameira</i> sp.	Harpacticoida		x
<i>Ameiropsis minor</i>	Harpacticoida		x
<i>Cyclopina</i> sp.	Cyclopoida		x
sp. 2	Cyclopoida		x
sp. 3	Cyclopoida		x
sp. 4	Cyclopoida		x
<b>Ostracoda</b>			
sp 1			x
sp 2			x
sp 3			x
<b>Polychaeta</b>			
Maldanid sp 1	Maldanadae	x	
<i>Branchinotogluma</i> sp.	Polynoidae	x	
Scale worm			x
Unknown polychaeta sp.1			x
Unknown polychaeta sp.2			x
Unknown polychaeta sp.3 (in tube on hydroida)		xxx	
<b>Gastropoda</b>			
<i>Shinkailepas</i> sp	Phenacolepadidae	x	
<b>Cnidaria</b>			
sp. 1	Actinaria		x
sp. 2	Alcyonacea		x
sp. 3	Hydroida		xxx
<b>Foraminifera</b>			
sp. 1	Cf. Hormosinidae		x

species were present (4 analyzed for stable isotopes). Species at the three other vent sites occupied a narrower range of carbon isotopic signatures (Table 2), except for the scale worm, *Branchinotogluma* sp., which was enriched in

$^{13}\text{C}$  (-8.1‰) compared to other species. An unidentified scale worm at Fault Shrimp site was similarly enriched in  $^{13}\text{C}$  (-6.6‰), compared to other members of its community (Fig. 2a). At Fault Shrimp site, the only vent site for which we obtained enough particulate organic matter for stable isotope analysis, a mixture of bacterial mat and detritus measured -26.5‰ for  $\delta^{13}\text{C}$  and 1.4‰ for  $\delta^{15}\text{N}$ , while sieved particles < 60  $\mu\text{m}$  were respectively -27.6‰ and 1.9‰ (Fig. 2).

Not all vent species were identifiable as primary consumers of an unidentified particulate organic matter source(s). One exception was the crab *Austinograea yunohana*, whose higher  $\delta^{15}\text{N}$  values at two locations (Table 2) indicate that predation makes a significant contribution to its diet. Isotopic differences between the crab and the possible prey species that were analyzed are less than one trophic level (0.5‰ for C and 3.4‰ for N; Post, 2002), suggesting that the crab is omnivorous. At Fault Shrimp site, *Alvinocaris* sp. was also slightly enriched in  $^{15}\text{N}$  (10.7‰), compared to other species, suggesting some omnivory.

At the Cnidaria site, on the inactive peak, stable isotope values for 3 of 4 deep-sea species analyzed (for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) were almost identical (Fig. 2), and approximately one trophic level (see above) away from the isotopic signature of the POM sampled near the seafloor (Fig. 2). The detrital organic matter from the sediments at this site appeared to make little contribution to faunal diets, with the exception perhaps of the harpacticoid *Tisbe furcata*. None of the analyzed samples corresponded to a potential food source for the soft coral.

## Discussion

There was a clear difference in community composition between the active and inactive peaks. The active hydrothermal sites hosted species-poor communities dominated by mobile decapod species that appear to be vent endemic. The inactive site hosted a non-vent deep-sea fauna mainly



**Table 2.** Stable carbon and nitrogen isotopic composition ( $\pm$  standard error) of organisms at three sites on the active peak of NW Rota-1 Volcano (n = number of analyzed individuals). Data from other sites in Figure 2.

**Table 2.** Composition en isotopes stables du carbone et de l'azote ( $\pm$  erreur standard) des organismes des trois sites sur le pic actif du volcan Rota-1 nord-ouest (n = nombre d'individus analysés). Données des autres sites sur la figure 2.

Site	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
Gastros	<i>Opaepele loihi</i>	$-13.5 \pm 0.7$	$9.5 \pm 0.2$	7
	<i>Shinkailepas</i> sp.	-15.5	8.0	1
Scarp Top	<i>Opaepele loihi</i>	$-12.3 \pm 0.5$	$10.1 \pm 0.2$	8
	<i>Austinograea yunohana</i>	$-13.9 \pm 1.5$	$11.8 \pm 0.2$	3
	<i>Branchinotogluma</i> sp.	$-8.1 \pm 0.5$	$9.5 \pm 0.4$	4
Shimmering Shrimp	<i>Opaepele loihi</i>	$-13.6 \pm 0.5$	$9.3 \pm 0.3$	16
	<i>Austinograea yunohana</i>	$-13.7 \pm 0.8$	$12.0 \pm 0.0$	2

dominated by hydroids and amphipods, and had an abundant and diverse meiofauna in comparison to the vent sites.

The abundant faunal biomass at hydrothermal vents is a source of food for a variety of endemic and non-vent predators (Voight, 2000). Nevertheless it was unexpected to find evidence for two consumer trophic levels at these newly colonised vents with few species. Deep-sea hydrothermal vent communities at early stages of development tend to be dominated by suspension and deposit feeders, while other functional groups such as carnivores typically appear at later succession stages (Shank et al., 1998; Levesque et al., 2006). The ability to switch feeding modes may be advantageous at this unstable site. The isotopic evidence for predation by the crab *Austinograea* on small-sized *Opaepele loihi* shrimp is supported by the *in situ* behaviour of the shrimp; in the presence of crabs, they exhibited 'explosive' evasion manoeuvres. A potential predator-prey relationship between *Austinograea* crabs and shrimp was reported from another deep-sea hydrothermal vent at the Central Indian Ridge (van Dover, 2002). Bythograeid crabs are able to supplement their diet by scavenging and detritivory (Martin et al., 1998) and have specialized setae for cropping bacterial mats (V. Tunnicliffe, personal observation). The Alvinocarid shrimp also appear to feed at more than one trophic level. *Alvinocaris* sp. nov. from Fault Shrimp site were slightly enriched in  $^{15}\text{N}$  and depleted in  $^{13}\text{C}$ , compared to other species, indicating an omnivorous diet, possibly composed of a mixture of  $^{13}\text{C}$ -depleted organic material and small invertebrates.

A mixed diet of predation and grazing/detritivory accounts for some of the apparent food partitioning observed at the more species-rich vent sites. The broad range in carbon isotopic values at Scarp Top and Fault Shrimp sites is also indicative of multiple sources of primary production. A simple mixing model with two end-

member carbon sources offers the most parsimonious explanation for the positioning of the various species and organic detritus across the observed range in  $\delta^{13}\text{C}$  values. One source is assumed to be at the enriched end of the range, near the  $\delta^{13}\text{C}$  values of the scale worms ( $-6.6$  to  $-8.1\text{‰}$ ), while the other source is assumed to be depleted in  $^{13}\text{C}$ , near the values observed for the fine particles and microbial mat ( $< -27.5\text{‰}$ ) sampled at Fault Shrimp site. A biogeochemical explanation for this two end-member model can be found in the observation that chemolithoautotrophic microbes using the two different forms of the  $\text{CO}_2$  fixing enzyme, Ribulose Biphosphate Carboxylase/Oxydase (Form I and Form II), produce organic matter with an approximately 20‰ difference in carbon isotope values (Robinson et al., 2003). Both forms of Rubisco have been recorded at hydrothermal vents but studies have been limited to microbial endosymbionts of vent invertebrates (Robinson et al., 2003). There are presently no data available on the occurrence of Rubisco forms I and II among free-living, chemoautotrophic microorganisms at vents. The two forms are known to occur in free-living photosynthetic microorganisms including a cyanobacterium (form I) and a nonsulfur purple photosynthetic bacterium (form II) (cited in Robinson et al., 2003). End-member chemosynthetic organic matter sources at the NW Rota-1 vents would need to have a  $\delta^{15}\text{N}$  value of around 6.0 to explain observed values in consumer species. None of the organic detritus or microbial mat samples from the vent sites had stable isotope signatures that approached either proposed end member. This 'missing end-member' problem has been encountered in other hydrothermal vent food web studies (Van Dover, 2002). The end-member organic matter source for the non-symbiotic fauna at vents could be quickly turned over by grazers. The more refractory material that dominates particulate detritus does not then mirror the actual food source available to consumers.

Food partitioning has been previously reported in vent communities and may be an important structuring factor (Levesque et al., 2006). In this study, food partitioning was especially pronounced between the co-occurring Alvinocarid shrimp, *Opaepele loihi* and *Alvinocaris* sp. nov. which had very different  $\delta^{13}\text{C}$  signatures at Fault Shrimp site. Both scale worms were nonetheless enriched in carbon compared to the vent other species, and may selectively feed on the  $^{13}\text{C}$ -enriched end member. This is consistent with observations of the scaleworm *Branchinotogluma* sp. at other vent sites, which graze directly on the microbial mats that grow around vent openings (Levesque et al., 2006).

On the inactive peak, most of the macrobenthic species had overlapping  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures that indicated direct utilization of suspended particulate organic matter as a major food source. This is likely descending material from the photic zone; plankton from a vertical net tow from 100 m depth to the surface over nearby West Rota Volcano had exactly the same  $\delta^{13}\text{C}$  value (-21.6‰) as the near bottom suspended material sampled on NW Rota-1 (550 m depth). In addition, the amphipod guts contained visible orange-pigmented material, suggesting that their food source contained carotenoids (i.e. photosynthetically synthesized material). The carbon isotopic signature of the infauna differed; one of the dominant harpacticoid species was relatively depleted in  $^{13}\text{C}$  compared to the larger macrobenthic species. It may rely on a mixture of descending material and the more refractory organic carbon sampled from the surface sediment.

## Conclusions

Chronic perturbation by on-going volcanism excluded the more complex, photosynthetically-based, deep-sea sessile community from the active peak of NW Rota-1 Volcano, even away from the areas of venting. The simple vent community and food web are typical of post-eruptive vent habitats, while the unusual dominance by mobile macrofauna reflects habitat instability. The slightly more complex community and food web at Fault Shrimp site, where venting occurred through cemented lavas, underline the importance of substratum stability to the vent fauna. The near-absence of meiofauna at these vents and their abundance and diversity at the nearby Cnidaria site point to the importance of organic matter accumulation for the establishment of meiofaunal communities on the volcanic substratum. Evidence for food partitioning and multiple organic matter sources indicates that these are fundamental features of even chronically disturbed vent communities.

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