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Peripheral communities of the Eastern Lau Spreading Center and Valu Fa Ridge: community composition, temporal change and comparison to near-vent communities

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Abstract

Western Pacific hydrothermal vents will soon be subjected to deep-sea mining and peripheral sites are considered the most practical targets. The limited information on community dynamics and temporal change in these communities makes it difficult to anticipate the impact of mining activities and recovery trajectories. We studied community composition of peripheral communities along a cline in hydrothermal chemistry on the Eastern Lau Spreading Center and Valu Fa Ridge (ELSC-VFR) and also studied patterns of temporal change. Peripheral communities located in the northern vent fields of the ELSC-VFR are significantly different from those in the southern vent fields. Higher abundances of zoanthids and anemones were found in northern peripheral sites and the symbiont-containing mussel *Bathymodiolus brevior*, brisingid seastars and polynoids were only present in the northern peripheral sites. By contrast, certain faunal groups were seen only in the southern peripheral sites, such as lollipop sponges, pycnogonids and ophiuroids. Taxonomic richness of the peripheral communities was similar to that of active vent communities, due to the presence of non-vent endemic species that balanced the absence of species found in areas of active venting. The communities present at waning active sites resemble those of peripheral sites, indicating that peripheral species can colonize previously active vent sites in addition to settling in the periphery of areas of venting. Growth and mortality were observed in a number of the normally slow-growing cladorhizid stick sponges, indicating that these animals may exhibit life history strategies in the vicinity of vents that differ from those previously recorded. A novel facultative association between polynoids and anemones is proposed based on their correlated distributions.

Introduction

The deep-sea benthos is a species-rich environment (Hessler & Sanders 1967; Sanders 1968; Sanders & Hessler 1969; Wolff 1977; Grassle 1991; Gray *et al.* 1997). Despite the surprisingly large numbers of species found in the deep sea, biomass tends to be low, peaking at the shelf edge and then decreasing rapidly with depth (Lampitt *et al.* 1986; Rex *et al.* 2006). The low biomass in the deep sea has been attributed to the spatial and temporal separation of the deep sea from primary production at the sea surface and the resultant low rates of food supply (Sanders & Hessler 1969). However, there are some noteworthy exceptions to the general rule of low biomass in the deep sea such as the chemosynthesis-based communities found around hydrothermal vents, cold seeps and other reducing environments. In these habitats, localized energy sources and abundant primary production provide ample energy to fuel dense assemblages of megafauna. Hydrothermal vent fluid is seawater that has been circulated through the earth's crust, and is heated and stripped of oxygen, but enriched in heavy metals and reduced chemicals such as sulfides. Some bacteria can harness the energy in the reduced inorganic compounds and use it to fix inorganic carbon and therefore form the base of the hydrothermal vent food web. These bacteria can either be free-living or form symbiotic associations with a variety of metazoans that in turn often reach impressive sizes and contribute to the high biomass associated with hydrothermal vents (Childress & Fisher 1992; Van Dover 2000).

However, life at hydrothermal vents comes with a cost for metazoans. Vent fluid is anoxic and hot, ranging to well above the temperatures that metazoans can tolerate: ~400 °C (Spiess *et al.* 1980; Edmond *et al.* 1982; Pörtner 2002; Dilly *et al.* 2012; Ravaux *et al.* 2013). Furthermore, vent fluids can be quite toxic, containing high concentrations of compounds such as hydrogen sulfide that is lethal to many animals in even very low concentrations (Corliss *et al.* 1979; Lilley *et al.* 1983; Beauchamp *et al.* 1984; Johnson *et al.* 1986). This creates an environment where the highest levels of primary production occur in areas that are toxic to most animals. As a result, animal distributions at vents are correlated with levels of exposure to vent fluid, which is linked to their physiological tolerances, and in the case of animals with symbionts, their requirements for vent fluid. Faunal zonation patterns correlated with exposure to vent fluids have been documented on the East Pacific Rise (Hessler *et al.* 1985; Jollivet 1996; Shank *et al.* 1998; Mills *et al.* 2007; Matabos *et al.* 2008), Juan de Fuca Ridge (Sarrazin *et al.* 1997; Sarrazin & Juniper 1999; Bates *et al.* 2005), Central Indian Ridge (Van Dover 2001; Nakamura *et al.* 2012), Mid-Atlantic Ridge (Copley *et al.* 1997; Gebruk *et al.* 2000a,b; Cuvelier *et al.* 2009), the Okinawa Trough (Tokeshi 2011), the East Scotia Rise in the Southern Ocean (Marsh *et al.* 2012) and on the back arc spreading centers of the Western Pacific (Both *et al.* 1986; Desbruyères *et al.* 1994; Podowski *et al.* 2009, 2010; Kim & Hammerstrom 2012; Sen *et al.* 2013).

In addition to zonation within active vent fields related to differing levels of direct exposure to vent fluid, two major zones have been identified at the larger scale of a vent field: a near-vent or central zone, centered around areas with robust hydrothermal emissions inhabited by symbiont-containing fauna and associated vent endemic fauna, and an outlying zone largely removed from direct impact from venting fluid that is inhabited by normal background deep-sea fauna, but at greater densities than the surrounding deep sea (Hessler *et al.* 1985, 1988; Tunnicliffe *et al.* 1985, 1986; Fisher *et al.* 1994). There is a mixed zone in between that has been referred to as the distal, intermediate and median zone. This zone is inhabited by both vent endemic and non-vent endemic fauna, while in the outer zone further away from sources of venting, the majority of the animals present are non-vent endemic deep-sea species (Arquit 1990; Sudarikov & Galkin 1995; Kim & Hammerstrom 2012). The distances of these latter zones from sources of intense venting differs among vent fields and can range from tens of meters to kilometers. Considerably less work has focused on the communities present in the peripheral zone than on the central zone and its vent endemic populations (Boschen *et al.* 2013). However, despite the abundance of background species, these communities are different from the surrounding deep-sea community. They tend to host higher biomass densities, which is likely due to their proximity to vents and the high primary productivity associated with them (Lonsdale 1977; Arquit 1990; Galkin 1997).

Western Pacific vents are of immediate interest because they are currently targeted for deep-sea mining of polymetallic sulfides (Halfar & Fujita 2002; Van Dover 2011; Boschen *et al.* 2013). Peripheral areas some distance away from active vents could be the main targets for mining because they have lower biomass and seemingly less distinctive fauna (Hoagland *et al.* 2010), and are less hazardous than active vents (Halfar & Fujita 2002). One goal of this study was to better characterize the peripheral communities of Western Pacific vents and explore variation in these communities on the Eastern Lau Spreading Center and Valu Fa Ridge (hereafter Lau Basin or ELSC-VFR). In this system, geology, topography and fluid chemistry change along a north–south gradient due to differing distances from the active volcanic arc (Taylor *et al.* 1996; Martinez *et al.* 2006; Ferrini *et al.* 2008; Mottl *et al.* 2011) and these changes have been linked to differences in animal communities in central zones of the vent fields (Podowski *et al.* 2010; Beinart *et al.* 2012; Sen *et al.* 2013). We hypothesized that, similar to near-vent communities, the community composition of peripheral sites in the northern portion of the Lau Basin would differ from that of southern peripheral sites.

A second goal of this study was to document natural patterns of temporal change in peripheral sites. Based on the results obtained from the study of succession and temporal change in sites of active venting (Sen *et al.* 2014), we expected changes in fluid chemistry to cause major changes in community composition or recruitment and turnover of species in peripheral sites. Studying temporal change in peripheral communities additionally provided the opportunity to study later stages of the successional model proposed for vent communities of the Lau Basin in more detail. This type of data will be critical to evaluating environmental impact assessment plans and recovery trajectories when mining of deep-sea hydrothermal vents begins in this region.

Material and Methods

Location and study sites

The Eastern Lau Spreading Center and Valu Fa Ridge (ELSC-VFR) are located in the Western Pacific Ocean between the island nations of Fiji and the Kingdom of Tonga. They are situated between a remnant arc (Lau Ridge) and an active volcanic arc (Tofua Volcanic Arc), west of the Tonga-Kermadec Trench. Six vent fields have been visited and imaged along the ~230-km length of the ELSC-VFR. From north to south, these vent fields are Kilo Moana, Tow Cam, ABE, Tu'i Malila, Mariner and Vai Lili. Peripheral assessment sites were identified and studied from the four northernmost vent fields. Kilo Moana and Tow Cam are characterized by deep axial basins with lobate basaltic substrates that have a boulder-like appearance. ABE and Tu'i Malila are shallower and host a mixture of basalts and andesites, resulting in a more friable substrate (Ferrini *et al.* 2008). Peripheral assessment sites were chosen based on the presence of elevated concentrations of megafauna in areas without obvious hydrothermal venting, located in a terrain suitable for investigation using a remotely operated vehicle (ROV). Each peripheral assessment site was named with a two- or three-letter acronym for the vent field followed by a sequential number and the letter P to denote peripheral sites and distinguish it from active vent or edifice assessment sites within the same vent field (Podowski *et al.* 2010; Sen *et al.* 2013). Two peripheral assessment sites from Kilo Moana (KM1P and KM2P), one from ABE (ABE1P) and one from Tu'i Malila (TM1P) were identified in 2005 and marked by the deployment of weighted syntactic foam markers. In 2006 all these assessment sites were imaged along with three additional peripheral sites; a second site from ABE (ABE2P) and two from Tow Cam (TC1P and TC2P). In addition to images, physico-chemical measurements were taken at each site in 2006. Markers were not deployed at the two new Tow Cam sites, thereby preventing a return visit to these assessment sites. However, in 2009, all the other sites were re-imaged and re-surveyed. Supporting Information Figs S1–S4 show the locations of each peripheral assessment site in relation to edifices and active vent assessment sites in each vent field.

Imagery and georeferencing

All data were collected with the ROV *Jason II* aboard the R/V *Melville* in 2006 and aboard the R/V *Thomas G. Thompson* in 2009. Images were collected using a down-looking Nikon Coolpix Insite Scorpio digital still camera mounted on the ROV as described by Podowski *et al.* (2010). A series of lines of overlapping photographs were obtained with at least 25% overlap between each line of images. Images were taken from 2 or 5 m above the sea floor in 2006 and from an intermediate distance of 3 m above the sea floor in 2009 using the same heading as in 2006. The photographs of each assessment site were then stitched together to create seamless mosaics of the entire assessment site using a customized MATLAB script (Pizarro & Singh 2003; Singh *et al.* 2004).

The location of each assessment site on the sea floor was determined using Jason's long base line navigation system and precisely navigated sea-floor transponders. This allowed re-location of the assessment sites in subsequent years. However, navigation during acquisition of images at each assessment site was accomplished using a closed-loop system based on an acoustic Doppler velocity navigation system. This system allows navigation with cm-scale accuracy over the distances and time spans necessary for documentation of an assessment site. Photomosaics from 2009 were georeferenced by using the navigation data associated with the individual images (synchronized using time stamps on the images) that comprised the finished mosaic (procedure outlined in Podowski *et al.* 2009, 2010) in ARCMAP 10.0 and 10.1, using the WGS 1984 UTM 1S co-ordinate system. Because of navigational offsets between years, the 2006 photomosaics were georeferenced directly to the 2009 photomosaics using recognizable features common to both mosaics (Sen *et al.* 2014). Areas imaged in 2009 were generally larger than in 2006. Only areas in common were used for the analyses reported here.

Faunal identifications and digitization

After photomosaics were georeferenced, locations of all faunal groups were digitized in ARCMAP 10.0 and 10.1. Fauna were either digitized as points, where one point represented one individual of a particular taxon, or as polygons, enclosing aggregations of individuals that are difficult or impossible to enumerate. The symbiont-containing fauna, *Ifremeria nautilei* and *Bathymodiolus* *brevior,* as well as zoanthids and barnacles were digitized as polygons. Octocoral colonies were digitized as polygons as the area of a colony provides a better indicator of the amount of coral present than the number of separate colonies. Only one apparent morphospecies of octocoral was observed in this study; however, it was not collected and is therefore referred to as 'unidentified octocoral'. Similarly, the single morphospecies of zoanthid present has not been identified and is referred to as Zoanthidea sp. (Zelnio *et al.* 2009). Several barnacle genera are present on these spreading centers but most could not be distinguished in the photographs and all non-stalked barnacles were grouped together as 'barnacles'.

All other faunal groups were digitized as points where each individual was marked. Identifications were made to the lowest possible taxon. The taxa that could be reliably identified to the species level included the squat lobster *Munidopsis lauensis,* the anomuran crab *Paralomis hirtella,* the snails *Thermosipho desbruyeresi* and *Phymorhynchus* sp., the holothurian *Chiridota hydrothermica,* the zoarcid fish *Thermarces* sp., the polynoids *Branchinotogluma* sp. nov. and *Levensteiniella raisae,* the stick sponge *Asbestopluma* sp., the lollipop sponge *Abyssocladia dominalba,* the brisingid seastar, *Freyella* sp. and the anemone *Chondrophellia orangina.* A single morphotype of white ophiuroid was present at one site and is referred to as such. Similarly, the only individual imaged from the class Pycnogonida is referred to as pycnogonid. Polynoids of the subfamily Harmothoinae could not be identified to the species level but could be distinguished from other polynoid genera and were categorized as Harmothoinae. Two species of brachyuran crabs, *Austinograea alayseae* and *Austinograea williamsi,* are known to inhabit Lau vents, but cannot be reliably distinguished from dorsal images and were grouped together as *Austinograea* spp. Similarly, the shrimp taxa could not be reliably differentiated and were treated as a single taxon (shrimp). In addition to the zoanthids, a number of different species of anemones have been described from the Lau Basin, including *Cyananthea hourdezi*, *Alvinactis chessi, Sagartiogeton erythraios, Chondrophellia. orangina*, *Amphianthus* sp. and Actinostolidae sp. (Zelnio *et al.* 2009). *Chondrophellia orangina* has distinctive orange coloration and was easily identified. All anemones other than Zoanthidae sp. and *C. orangina* were treated collectively as 'anemones' for consistency.

Physico-chemical data

In situ voltammetry and a thermocouple were used to measure hydrogen sulfide and oxygen concentrations and temperatures at a number of locations with visible indications of hydrothermal venting (presence of shimmering water detectable from close proximity or dense aggregations of fauna) in each assessment site in 2006 and 2009 (Luther *et al.* 2000, 2008; Podowski *et al.* 2009). Approximately 20 discrete measurements were taken at each assessment site in 2006. At each location, four to seven scans of sulfide and oxygen concentrations were taken, with temperature recorded during each scan. For each distinct location, average, maximum and minimum values of all three parameters were obtained from the multiple scans. In 2009, we attempted to duplicate the 2006 measurement locations for the KM1P and KM2P assessment sites. However, fewer measurements were made at the ABE and TM1P assessment sites in 2009. Local ambient temperature for each vent field in each year was determined from the ROV's Conductivity, Temperature and Depth (CTD) data and subtracted from the spot temperatures measured to obtain the temperature anomaly at each location (Podowski *et al.* 2009, 2010; Sen *et al.* 2014).

Statistical and temporal analyses

After all faunal groups were digitized, the abundance or area covered by each taxon was determined through queries in ARCMAP 10.1. If large changes were detected between years, the original images were re-examined to confirm that the results were not an artifact of image quality differences or distortions caused by the georeferencing procedure. Similarly, other notable findings, such as no movement by anemones between years or rapid growth of sponges were confirmed by examination of the original images. In order to test whether the changes observed in the aggregated faunal communities were significant, Chi-squared tests were conducted using the 2006 percent coverage as the expected values and the 2009 percent coverage as the observed values.

Alpha diversity (total number of taxa) was recorded for each peripheral assessment site in both years of study. In order to examine species turnover between visits, the Wilson–Shmida index of beta diversity was calculated, using the presence and absence of the taxa in the 2 years of study. This index is calculated by dividing the sum of the number of taxa gained and lost between 2006 and 2009 by the mean taxonomic richness of both years, multiplied by 2 (Wilson & Shmida 1984). Bray–Curtis similarity indices based on a fourth root transformation of densities of faunal groups was calculated in PRIMER 6.0 (PRIMER-E, Plymouth, UK) for each assessment site to complement the Wilson–Shmida index of beta diversity in assessing temporal variation. The aerial coverage of the aggregated fauna was converted to density based on average sizes of a single individual of the faunal group. Table 2 lists the density of all the faunal groups at every site included in this study, which was used for the construction of the Bray–Curtis similarity indices. Overall peripheral fauna diversity (total number of taxa across all peripheral sites) was calculated for each year of study as well as for both years combined.

The Bray–Curtis resemblance matrix was used for cluster analysis with PRIMER 6.0. Two types of cluster analyses were conducted. The first used only the peripheral assessment sites and the second used the previously characterized active vent and edifice assessment sites with the peripheral assessment sites. We expected the northern sites to cluster separately from the southern sites and we used ANOSIM (Analysis of Similarity) to determine if this clustering was significant. Clustering of the three types of assessment sites (active lavas, edifices and peripheral sites) was also tested for significance using ANOSIM. SIMPER (Similarity Percentages) analysis was conducted to determine which faunal groups contributed the most towards the similarities within and between clusters.

Visual inspection of the mosaics suggested that polynoid worms occurred preferentially near anemones. To test this hypothesis, polynoid distributions were compared to the null model of random distribution within each assessment site. Anemones were digitized as points, and the area within each assessment site that constituted anemone substrate was calculated. This was done by measuring the diameters of five randomly chosen anemones with their tentacles fully extended from each site where polynoids were present and averaging these to obtain the average diameter of a fully extended anemone. Circles of this diameter (11 cm) were created around each anemone point and any polynoids within these circles were classified as associated with anemones. Within an assessment site, all the circles around anemone points were summed to obtain the total available anemone substrate. If polynoids were randomly located and showed no preference for anemone substrate, then the proportion of polynoids associated with anemones should be equivalent to the proportion of anemone substrate in an assessment site. For example, if 10% of the area of a site was anemone substrate, then we expected 10% of the polynoids present at the site to be located on anemone substrate by random chance alone. To determine if the polynoid species exhibited a preference for association with anemones, a Chi-squared test was used to test for significant differences between the expected distribution and the observed distribution.

Results

Peripheral communities

In 2006 there was thermal evidence of venting at all of the peripheral assessment sites; however, sulfide was either absent or below the level of detection at all but one site that year (Table 1). At KM1P and KM2P temperature was at least slightly elevated at all measurement locations (average temperature anomaly 0.1–3.3 °C in 24 locations and 0.2–5.3 °C in 28 locations, respectively), but sulfide was not detected at any location. Similarly, temperatures were slightly elevated at all locations surveyed at ABE1P and ABE2P (0.7–2.5 °C in 20 locations and 0.6–2.3 °C in 19 locations, respectively) but sulfide was never detected. At TC1P, seven out of a total of 13 measurements indicated small degrees of hydrothermal venting (0.1–0.8 °C temperature anomaly) and sulfide

Table 1. Summary of physico-chemical measurements taken at the peripheral assessment sites in the 2 years of the study.

site	year	total number of physico-chemical measurements	ambient temperature (°C)	number of positive temperature anomalies	range of positive temperature anomalies (°C)	number of measurements of detectable sulfide	range of detectable sulfide concentrations ($\mu mol \cdot l^{-1}$)
KM1P	2006	24	2.3	24	0.1–3.3	0	N/A
	2009	22	2.3	0	N/A	15	0.1–2.2
KM2P	2006	28	2.3	28	0.2–5.3	0	N/A
	2009	28	2.3	22	0.1–7.6	10	0.1–5.3
TC1P	2006	13	2.4	7	0.1–0.8	0	N/A
	2009	0	2.3	N/A	N/A	N/A	N/A
TC2P	2006	11	2.4	2	0.1–2.8	11	0.1–1.4
	2009	0	2.3	N/A	N/A	N/A	N/A
ABE1P	2006	20	2.4	20	0.7–2.5	0	N/A
	2009	5	2.4	3	0.2–1.2	0	N/A
ABE2P	2006	19	2.4	19	0.6–2.3	0	N/A
	2009	5	2.4	2	0.1–0.2	0	N/A
TM1P	2006	23	2.5	23	0.4–12.5	0	N/A
	2009	9	2.5	8	0.2–3.1	0	N/A

KM = Kilo Moana; TC = Tow Cam; TM = Tu'i Malila; P = peripheral site; N/A = not applicable.

was not detected at any location at this site. At TC2P, only two of 11 temperature measurements were above ambient (0.1 and 2.8 °C temperature anomaly); however, low concentrations of sulfide were detected at all locations where measurements were taken at this site (0.1–1.4 μM). The highest temperatures were recorded at TM1P, where all 23 measurements recorded elevated average temperatures (temperature anomaly: 0.4–12.5 °C), but no detectable sulfide.

Zoanthids dominated the communities at the majority of the assessment sites (Table 2, Fig. 1), although they were more abundant in the northern sites. Among the symbiont-containing gastropods that form large aggregations in near-vent communities, only sparse, small aggregations of *Ifremeria nautilei* were seen at peripheral sites. *Bathymodiolus brevior* was present in the northern peripheral sites, but was absent from southern peripheral sites. Sponges followed the opposite trend and were abundant in southern peripheral sites but were absent from the northern sites.

The overall community composition was different between the northern and southern peripheral assessment sites (global R = 0.961, P = 0.002, Fig. 2). Within each cluster, there is additional clustering that corresponds to the individual vent fields. The average similarity within the northern group was 63%, with anemones, the squat lobster *Munidopsis lauensis* and Zoanthidea sp. contributing the most to similarities among sites (Table 3). Within the southern group, the average similarity was 69% and *Asbestopluma* sp., shrimp and *M. lauensis* contributed the most to the similarity among sites. The average similarity between the northern and southern groups was 40%, with anemones, the cladorhizid sponge *Asbestopluma* sp. and Harmothoinae contributing the most to the dissimilarity between the northern and southern groups. Other notable differences between the northern and southern sites included the absence of the symbiont-containing mussel *Bathymodiolus brevior*, all three polynoid species, the anomuran crab *Paralomis hirtella* and the brisingid seastar *Freyella* sp. from the southern peripheral assessment sites.

The observed distribution of the polynoids *Branchinotogluma* sp. nov. and *Levensteiniella raisae* was significantly different from what would be expected if they were randomly distributed (P < 0.001 for both species). The observed distribution of polynoids of the subfamily Harmothoinae did not differ significantly from the expected distribution (P = 0.57). Anemones and the areas covered when their tentacles were fully extended ('anemone substrate') constituted 8% of the available substrate at the KM1P site in 2006. One of the two individuals of *Branchinotogluma* sp. nov., the one individual of *L. raisae* and none of the nine individuals of Harmothoinae were associated with anemones. In 2009, no individuals of *Branchinotogluma* sp. nov. and *L. raisae* were present at this site and none of the six individuals of Harmothoinae was associated with anemones. At the KM2P site in 2006, 24% of the total available substrate constituted 'anemone substrate'. Fifty-eight per cent of *Branchinotogluma* sp. nov. (14 of 24 individuals), 54% of *L. raisae* (seven of 13 individuals) and 20% of Harmothoinae (one of five individuals) were associated with anemones. In 2009 the numbers of anemones at this site had decreased slightly, and noticeably fewer polynoids were visible. The single *Branchinotogluma* sp. nov. individual present in 2009 was associated with an anemone; however, only one of the nine *L. raisae* and none of the four Harmothoinae were associated with anemones. Three of the anemones in association with polynoids were identifiable as *Sagartiogeton erythraios* due to the black spots on the stalks of this species. However, in most cases it was not possible to identify the specific species of anemone associated with the polynoids. The association never involved the easily identifiable *Chondrophellia orangina.* Examples of polynoids located on anemones are shown in Fig. 3.

Comparison of peripheral communities to near-vent communities

Individual northern peripheral sites tended to have higher taxonomic richness than the active vent sites but were comparable in taxonomic richness to edifice assessment sites (Table 4). The total number of taxa documented at peripheral sites, 23, was the same as the overall diversity at active vent sites for both years combined. Slightly fewer taxa were visible on edifices (overall diversity of 20 for both years combined).

Peripheral communities were significantly different from the other two community types (Fig. 4), although the KM1 active vent site results for 2009 fell within those for the peripheral group (global R = 0.611, P = 0.001). The SIMPER analysis indicates that the active vent assessment sites and edifice assessment sites were more similar to each other than to peripheral assessment sites (average similarity 51%, Table 5). Shrimp, *Branchinotogluma segonzaci* and *Asbestopluma* sp. contributed the most to the dissimilarity between edifice and peripheral assessment sites while *Asbestopluma* sp., anemones and *Austinograea* spp. contributed the most to the dissimilarity between active vent and peripheral assessment sites. Peripheral assessment sites were more similar to the active vent assessment sites (39%) than edifice assessment sites (average similarity 31%).

There were several notable differences in the animal communities in the different habitats. As expected there were large differences in the abundance of symbiont-con-

Table 2. Density and coverage or abundance for all taxa imaged at peripheral sites in the Lau Basin vent fields. The fauna digitized as polygons (aggregated fauna) are indicated with an asterisk. The total area covered by the aggregated faunal groups (in m^2), or total number of individuals in the case of solitary faunal groups is given followed by the density per square meter in parentheses.

taxa	KM1P 2006	KM1P 2009	KM2P 2006	KM2P 2009	TC1P 2006	TC2P 2006	ABE1P 2006	ABE1P 2009	ABE2P 2006	ABE2P 2009	TM1P 2006	TM1P 2009
Ifremeria nautilei[a]	0.001 (0.000)	0.003 (0.000)	0.253 (0.010)	0.068 (0.003)	0.0019 (0.000)	0 (0)	0.003 (0.000)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Bathymodiolus brevior[a]	0.696 (0.038)	0.244 (0.013)	0.023 (0.001)	0.025 (0.001)	0 (0)	0.003 (0.000)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
barnacles[a]	0.346 (0.019)	0.015 (0.001)	0.220 (0.009)	0.173 (0.007)	0 (0)	0 (0)	0.184 (0.002)	0.255 (0.005)	0 (0)	0 (0)	0 (0)	0 (0)
Zoanthidea sp.[a]	3.636 (0.199)	4.893 (0.268)	14.738 (0.568)	16.836 (0.667)	4.321 (0.396)	3.790 (0.278)	0.080 (0.001)	0.019 (0.000)	0 (0)	0.016 (0.001)	0.302 (0.011)	0.196 (0.007)
unidentified octocoral[a]	0 (0)	0 (0)	0 (0)	0 (0)	0.002 (0.000)	0 (0)	0 (0)	0 (0)	0.001 (0.000)	0 (0)	0.037 (0.001)	0.0359 (0.001)
white flocculent bacteria[a]	0 (0)	0 (0)	0 (0)	0 (0)	0.267 (0.024)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
bacteria and Zoanthidea sp. mix[a]	0 (0)	0 (0)	0 (0)	0 (0)	0.072 (0.007)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
anemones	164 (8.988)	113 (6.193)	662 (25.531)	569 (22.544)	43 (3.941)	316 (23.169)	6 (0.077)	4 (0.051)	0 (0)	0 (0)	104 (3.650)	50 (1.755)
Chondrophellia orangina	3 (0.164)	3 (0.164)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	7 (0.089)	1 (0.031)	1 (0.031)	6 (0.211)	10 (0.351)
Abyssocladia dominalba	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	29 (1.018)	29 (1.018)
Asbestopluma sp.	0 (0)	0 (0)	0 (0)	0 (0)	19 (1.741)	107 (7.845)	182 (2.326)[b]	248 (3.169)	300 (9.357)	97 (3.025)	184 (6.458)	146 (5.124)
Austinograea spp.	2 (0.110)	0 (0)	19 (0.733)	5 (0.198)	0 (0)	0 (0)	0 (0)	0 (0)	4 (0.125)	1 (0.031)	4 (0.140)	1 (0.035)
Freyella sp.	0 (0)	5 (0.274)	0 (0)	0 (0)	3 (0.275)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Chiridota hydrothermica	6 (0.329)	14 (0.767)	7 (0.270)	5 (0.198)	1 (0.092)	0 (0)	1 (0.013)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Thermosipho desbruyeresi	2 (0.110)	2 (0.110)	1 (0.039)	0 (0)	0 (0)	0 (0)	2 (0.026)	0 (0)	1 (0.031)	1 (0.031)	1 (0.035)	0 (0)
Munidopsis lauensis	42 (2.302)	18 (0.986)	54 (2.083)	79 (3.13)	16 (1.466)	30 (2.200)	17 (0.217)	12 (0.153)	20 (0.624)	4 (0.124)	3 (0.105)	4 (0.140)
Paralomis hirtella	1 (0.055)	0 (0)	1 (0.039)	1 (0.040)	2 (0.183)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Branchinotogluma sp. nov.	2 (0.110)	0 (0)	24 (0.926)	1 (0.040)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Harmothoinae	9 (0.493)	6 (0.329)	5 (0.193)	4 (0.158)	9 (0.825)	4 (0.293)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Levensteiniella raisae	1 (0.055)	0 (0)	13 (0.501)	9 (0.357)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Phymorhynchus sp.	1 (0.055)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Pycnogonid	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.035)	0 (0)
shrimp	0 (0)	0 (0)	8 (0.309)	1 (0.040)	2 (0.183)	2 (0.146)	10 (0.128)	6 (0.077)	6 (0.187)	6 (0.187)	11 (0.386)	39 (1.369)
Thermarces sp.	0 (0)	1 (0.055)	1 (0.039)	1 (0.040)	0 (0)	0 (0)	3 (0.038)	1 (0.013)	2 (0.062)	1 (0.031)	0 (0)	1 (0.035)
white ophiuroid	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.035)	2 (0.070)
total area	18.247	18.247	25.928	25.928	10.912	13.639	78.262	78.262	32.061	32.061	28.491	28.491

KM = Kilo Moana; TC = Tow Cam; TM = Tu'i Malila; P = peripheral site.

[a] Fauna digitized as polygons (aggregated fauna).

[b] *Asbestopluma* sp. is likely underrepresented at ABE1P in 2006 because the images were dark and individuals were not clearly visible.

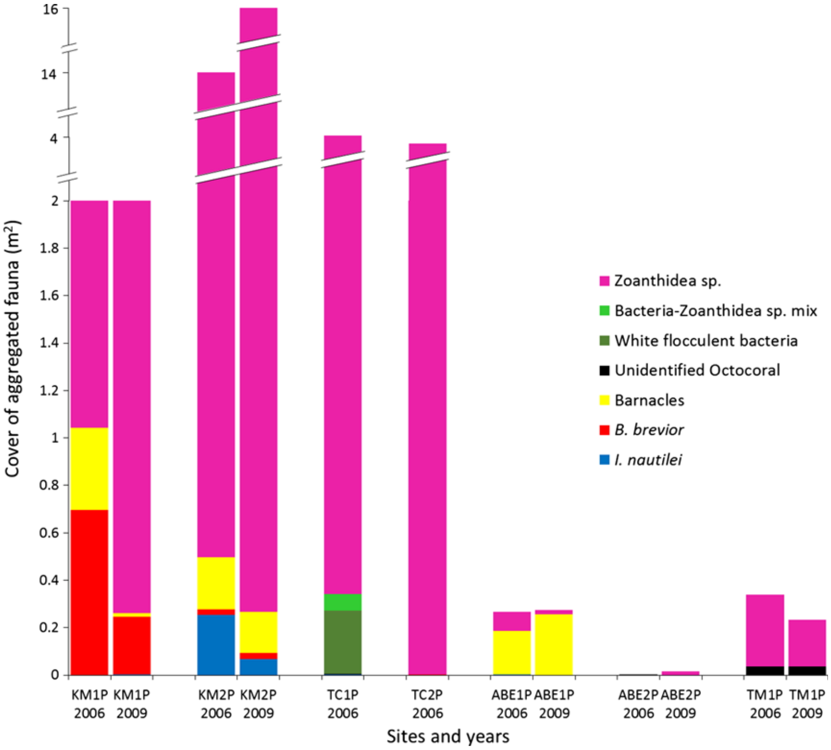

Fig. 1. Coverage of aggregated fauna in the peripheral assessment sites in the 2 years of study. Sites are listed from northernmost to southernmost from left to right.

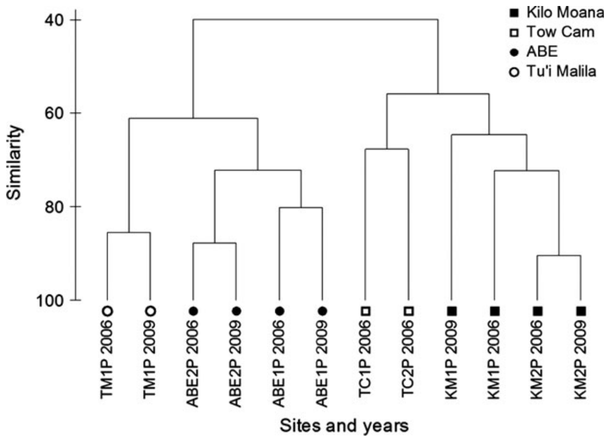

Fig. 2. Dendrogram based on average linkage Bray-Curtis similarity (fourth root transformed) of density of individuals of all faunal groups for all peripheral assessment sites. Squares represent assessment sites in the northern vent fields and circles represent assessment sites in the southern vent fields.

Table 3. Results of SIMPER analysis for the southern and the northern peripheral sites, as well as for the comparison between northern and southern sites. The faunal groups that contributed the most towards the average similarity within both northern and southern sites, as well as the species that contributed the most towards dissimilarity between northern and southern sites are listed.

faunal group	contribution towards similarity (%)	cumulative contribution (%)
northern peripheral sites (average similarity: 63.07)		
anemones	28.33	28.33
Munidopsis lauensis	18.76	47.09
Zoanthidea sp.	12.26	59.35
Harmothoinae	11.73	71.08
southern peripheral sites (average similarity: 68.74)		
Asbestopluma sp.	34.34	34.34
shrimp	15.74	50.08
Munidopsis lauensis	15.51	65.59
Chondrophellia orangina	7.67	73.26
comparison between northern and southern peripheral sites (average similarity: 39.85, average dissimilarity: 60.15)		
anemones	14.76	14.76
Asbestopluma sp.	11.53	26.28
Harmothoinae	8.42	34.71
Zoanthidea sp.	6.68	41.39

taining species between the active and peripheral sites. The symbiont-containing snail genus *Alviniconcha* was notably absent from all peripheral assessment sites and the other two symbiont-containing mollusks, *Ifremeria nautilei* and *Bathymodiolus brevior*, were rare or absent from the peripheral assessment sites. *Austinograea* spp. and shrimp were also present in higher abundances in the active sites than the peripheral sites. Edifices hosted some species of animals, such as the polynoid *Br. segonzaci* and paralvinellid worms, that were not seen on any of the active or peripheral assessment sites. The lollipop sponge *Abyssocladia dominalba*, the pycnogonid, the

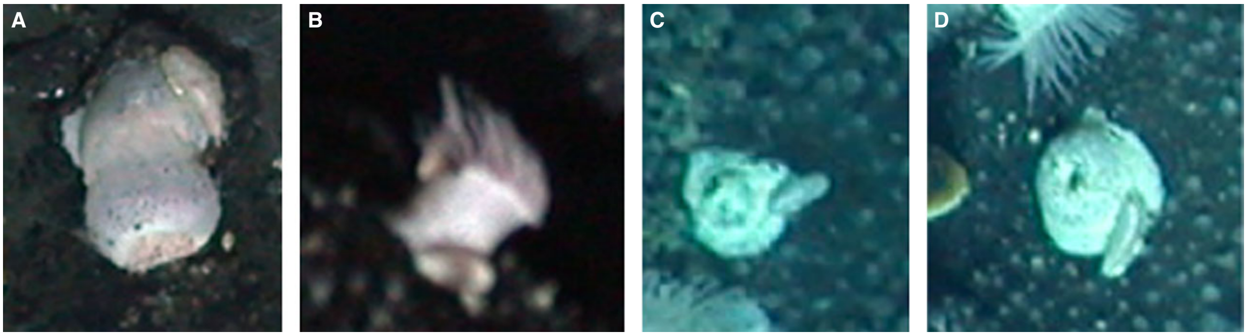

Fig. 3. Examples of polynoids on anemone bases at the two KM2P assessment sites. A: A *Levensteiniella raisae* polynoid on a *Sagartiogeton erythraios* anemone. B–D: *Levensteiniella raisae* polynoids on unidentified species of anemones.

Table 4. Diversity indices for vent, edifice and peripheral assessment sites in 2006 and 2009. Alpha diversity represents the total number of taxa recorded at a site during each year of sampling. Wilson-Shmida index of beta diversity was calculated as (g-l)/(2*average alpha diversity). Overall diversity is the total number of taxa recorded at each type of habitat (active vents, edifices and peripheral habitats).

site	alpha diversity		Wilson–Shmida index	Bray–Curtis similarity index	overall diversity		
	2006	2009			2006	2009	combined
vent sites							
KM1	9	10	0.42	76.4	18	18	23
KM2	12	9	0.14	88.8			
TC1	11	10	0.05	95.6			
TC2	7	7	0.36	83.3			
ABE1	11	10	0.14	91.0			
ABE2	10	8	0.17	92.3			
TM1	9	9	0.00	93.4			
edifice sites							
KM1C	14	12	0.12	75.5	19	13	20
TC1C	9	8	0.29	84.5			
ABE1C	13	11	0.17	84.5			
ABE2C	14	11	0.24	87.9			
ABE3C	11	7	0.22	60.7			
TM1C	7	8	0.20	81.9			
TM2C	11	9	0.35	62.0			
peripheral sites							
KM1P	15	12	0.26	69.1	22	21	23
KM2P	15	14	0.03	90.3			
TC1P	11	–	–	–			
TC2P	7	–	–	–			
ABE1P	10	8	0.22	80.2			
ABE2P	8	8	0.13	87.6			
TM1P	12	11	0.13	85.4			

KM = Kilo Moana; TC = Tow Cam; TM = Tu'i Malila; C = chimney; P = peripheral site.

unidentified white ophiuroid and the unidentified octocoral were only seen in peripheral sites and were absent from all active sites.

Temporal change in peripheral communities

KM1P appeared to experience a decline in venting between visits. None of the 22 measurements made at this site in 2009 recorded temperature anomalies above ambient (Table 1). However, small concentrations of sulfide were detectable at 15 of the locations (0.1–2.2 μmol l^{-1}). There was no significant change in venting at KM2P between visits detected with the thermocouple; 22 of 28 measurements were above ambient (0.1–7.6 °C) and sulfide was detectable at 10 of the locations (0.1–5.3 μmol l^{-1}). No physico-chemical data were obtained

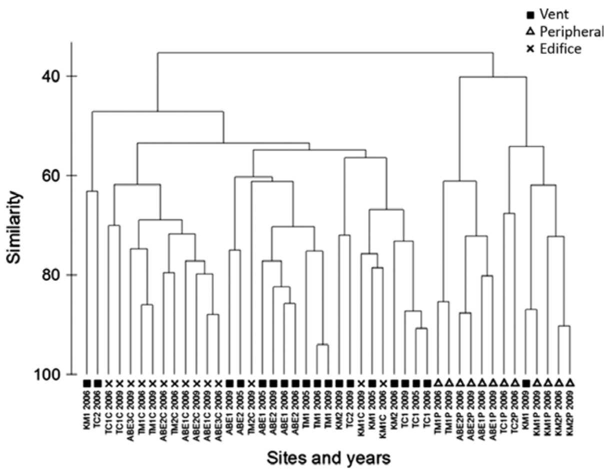

Fig. 4. Dendrogram based on average linkage Bray-Curtis similarity (fourth root transformed) of density of individuals of all faunal groups for all types of assessment sites.

from the TC peripheral sites in 2009. The remaining three sites were only surveyed briefly in 2009 due to time constraints; however, venting was detected, with similar temperature anomalies as in 2006. At ABE1P, three out of five measurements were above ambient (average temperature anomalies: 0.2, 1.1 and 1.2 °C), two out of five measurements at ABE2P were above ambient (0.1 and 0.2 °C) and eight out of nine measurements at TM1P were above ambient (0.2–3.1 °C). Sulfide was not detectable at any of the ABE or TM sites in 2009.

There were no large-scale changes in abundances or coverage of taxa at most of the peripheral sites between years. However, the two sites in the KM vent field both had reduced populations of symbiont-containing mollusks in 2009 and increased coverage of zoanthids. Barnacle coverage also decreased dramatically at KM1P (Fig. 1), the site with the largest detectable changes in thermal regime. This was the only peripheral assessment site where significant changes in the community were recorded between visits (P = 0.016). This site also had the highest Wilson–Shmida beta diversity and lowest similarity index between the 2 years of study (Table 4).

The numbers of anemones, *Asbestopluma* sp. and *Munidopsis lauensis* decreased at more than one site between years (Table 2). Site ABE1P was generally not well illuminated for imaging in 2006; however, inspection of the best images from this site in this year indicated that many of the sponges that were present in 2006 were absent in 2009. Growth and death of a number of individuals of *Asbestopluma* sp. was visible through the original images (Fig. 5). Large decreases were also seen in *Austinograea* spp. and *Branchinotogluma* sp. nov. at KM2P. *Munidopsis lauensis* and shrimp increased at KM2P and TM1P, respectively.

Table 5. Results of SIMPER analysis comparing the communities present in the peripheral, edifice and active vent assessment sites. The faunal groups that contributed the most towards the average dissimilarity between the different groups are listed.

faunal group	contribution towards dissimilarity (%)	cumulative contribution (%)
comparison between active vents and edifices (average similarity: 50.89, average dissimilarity: 49.11)		
shrimp	18.28	18.28
Branchinotogluma segonzaci	15.34	33.62
anemones	10.34	43.96
Munidopsis lauensis	6.7	50.66
comparison between active vents and peripheral sites (average similarity: 38.77, average dissimilarity: 61.23)		
Asbestopluma sp.	11.09	11.09
anemones	11.01	22.1
Austinograea spp.	9.72	31.81
shrimp	7.03	38.84
comparison between edifices and peripheral sites (average similarity: 30.92, average dissimilarity: 69.08)		
shrimp	15.48	15.48
Branchinotogluma segonzaci	11.59	27.07
Asbestopluma sp.	8.84	35.92
anemones	7.67	43.58

The *Chondrophellia orangina* anemones present in 2006 did not move detectably between years (Fig. 6). For other anemones, although many individuals moved between years, a number also appeared to remain in the exact same location over the 3-year period.

Discussion

Community variation along a north–south gradient

The geology, topography and fluid chemistry on the ELSC-VFR changes dramatically from north to south due primarily to the decreasing distances from the active volcanic arc (Taylor *et al.* 1996; Martinez *et al.* 2006; Ferrini *et al.* 2008; Mottl *et al.* 2011). The differences in rock and fluid chemistry could potentially affect the faunal communities associated with the spreading centers and indeed Podowski *et al.* (2010) and Sen *et al.* (2013) reported that communities associated with active venting differed substantially between the northern and southern vent fields. Beinart *et al.* (2012) also found differences in *Alviniconcha* species and holobiont combinations along a north–south gradient that they attributed to differences in the chemistry of the source fluids.

Similarly, there were significant differences in the composition of the peripheral communities present in the northern and southern vent fields. Anemones, including

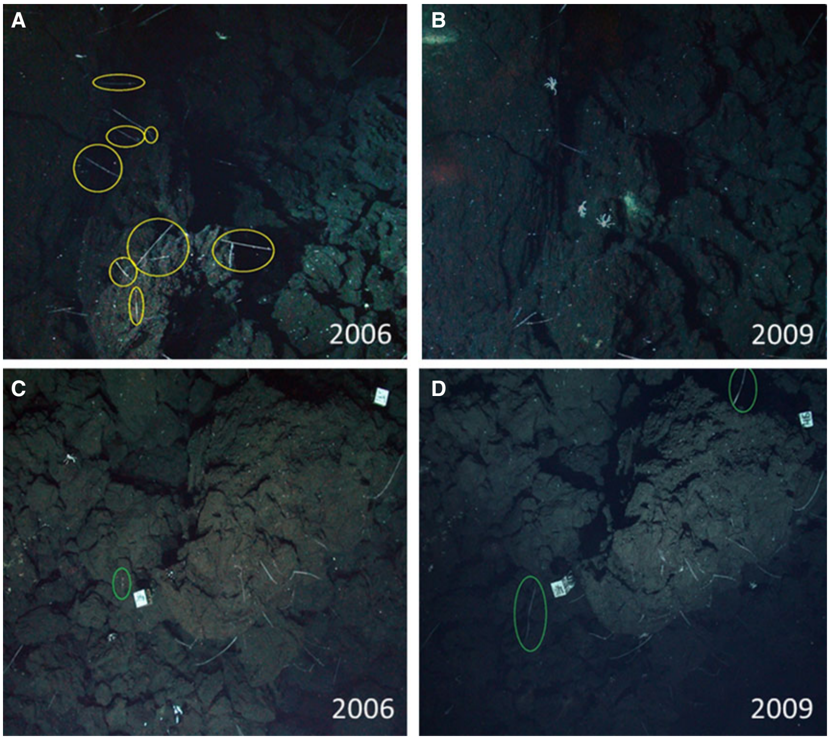

Fig. 5. Examples of *Asbestopluma* sp. in an area of the ABE2P assessment site in two different years. Sponges outlined in yellow disappeared from 2006 (A) to 2009 (B). Sponges outlined in green grew considerably from 2006 (C) to 2009 (D).

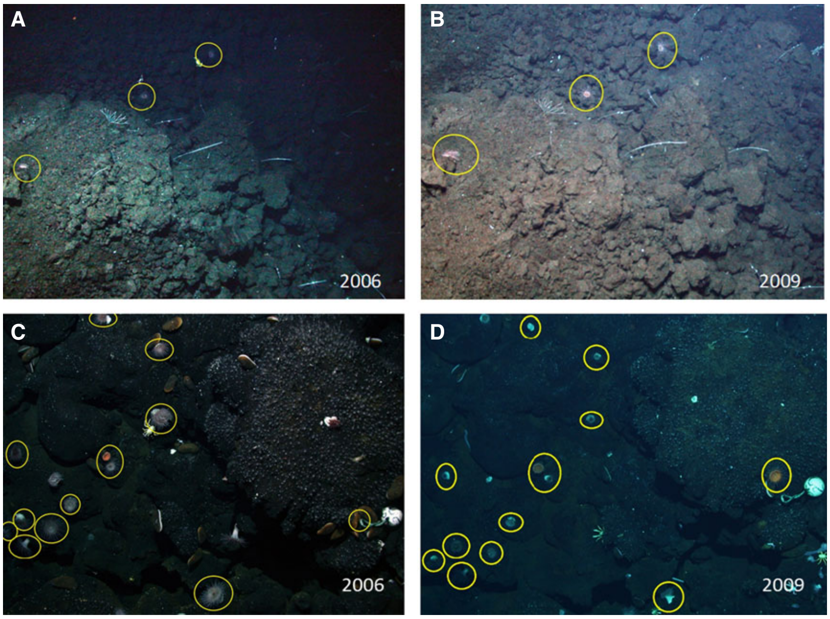

Fig. 6. Immobility of anemones. A and B: Examples of *Chondrophellia orangina* that have not changed position at the TM1P assessment site. C and D: Examples of anemones that have not moved at the KM1P assessment site, including two individuals of *C. orangina*.

zoanthids, were much more abundant in the northern sites. The highest density of zoanthids in the south was 5% that of the northern sites and most southern sites hosted densities less than 1% of what was measured in the north. Substrate could account for this difference, as suggested by Podowski *et al.* (2010), who proposed that the smooth surfaces of basaltic substrate in the northern sites could provide better anchorage for cnidarians than the friable andesitic lavas in the southern active vent assessment sites. More lateral diffusion of vent fluids occurs in the andesite-hosted southern sites (Podowski *et al.* 2010) and the pillow basalt substrates of the northern fields may also allow positioning near fluid sources with the benefit of access to the primary productivity associated with them, while facilitating avoidance of the fluid itself.

In addition to differences in substrate, differences in fluid chemistry could also be contributing to variable community composition along a north–south gradient. *Bathymodiolus brevior* mussels are absent from southern peripheral sites, despite being abundant in areas of more active hydrothermal flow in the southern vent fields (Podowski *et al.* 2010), some of which are only a few meters away from peripheral assessment sites. *Bathymodiolus brevior*, like all hydrothermal vent bathymodiolin mussels, harbors chemoautotrophic symbionts that require a reduced sulfur source to fuel chemoautotrophy and require access to sulfide-containing hydrothermal fluid to survive (Henry *et al.* 2008). It is likely that the low sulfide-to-temperature ratio of vent fluids in the southern vent fields in general (Podowski *et al.* 2010; Mottl *et al.* 2011; Sen *et al.* 2013) and the complete absence of detectable sulfide in the low temperature venting in the peripheral assessment sites found in this study are limiting the occurrence of the symbiont-containing mussels in southern peripheral sites. However, in the north, sulfide was often detected in very dilute hydrothermal fluid, and these low levels were sufficient to sustain at least some *B. brevior* individuals over the 3 years of this study.

A combination of factors could explain other observed patterns of community composition. The cladorhizid stick sponge *Asbestopluma* sp. was abundant in all of the southern assessment sites and only present in one northern site. Additionally, the cladorhizid lollipop sponge *Abyssocladia dominalba* and white ophiuroids were seen only in the southern-most site, TM1P. All three of these taxa were present in much higher abundances in the peripheral assessment sites than further afield on the Lau vents (A. Sen, C. R. Fisher & S. Kim, personal observations), suggesting a linkage to vent primary production, while their higher abundance in the south over the north suggests a concomitant sensitivity to sulfide.

With the exception of TC2P, northern peripheral assessment sites had higher taxonomic richness than the southern assessment sites. In their characterization of Lau vent communities, Kim & Hammerstrom (2012) also found that northern sites in general hosted higher diversities compared with southern sites. They suggested that despite multi-directional flow, the predominant northward flow in the region could contribute to the higher diversity in the northern sites, arguing that if a species first colonized a northern site, it would be less likely to expand its range southwards against the predominant currents. However, more detailed population genetic connectivity studies are needed to confirm this hypothesis, as the variations in geology, chemistry and bathymetry discussed above are also potential explanatory variables.

The proposed mining will likely alter fluid chemistry as well as substrate properties and as faunal distributions appear to be linked to these factors, mining operations could affect Lau communities in a number of ways and possibly change the ranges of certain taxa. The proposed mining scheme involves dewatering ores and returning the water to the sea floor. Crushing the basalt could affect settlement of zoanthids and other cnidarians, which might not be able to attach and anchor onto anthropogenically created crumbling surfaces. Another cause of concern is silt created during the harvesting of mineral-containing rocks on the sea floor. Debris could choke and clog the carnivorous sponges, cnidarians and filter feeders that inhabit Lau peripheral sites. The feeding style of cladorhizid sponges is well suited only to very calm environments because water movements can cause the extended, ensnaring filaments to entangle, which reduces trapping efficiency (Vacelet & Duport 2004).

Comparison of communities associated with active venting to peripheral communities

Peripheral communities are distinct from the active vent and edifice communities. Furthermore, communities on edifices and active vent sites are more similar to each other than either is to peripheral communities. A number of features contribute to the distinction between peripheral and near-vent communities. The most obvious is the lack of the fauna most tolerant of exposure to vent fluid, such as *Alviniconcha* spp., the polynoid *Branchinotogluma segonzaci* and paralvinellid worms, which are best adapted to the high temperatures and associated high productivity and low predation typical of the areas of most active diffuse flow on edifices (Tunnicliffe & Juniper 1990; Juniper *et al.* 1992; Juniper & Martineu 1995; Sarrazin *et al.* 1997; Sarrazin & Juniper 1999; McMullin *et al.* 2007; Sen *et al.* 2013). Similarly the other symbiont-containing mollusks, *Ifremeria nautilei* and *Bathymodiolus brevior*, were the biomass dominants in most active vent and edifice assessment sites and were either absent or present at low density in the peripheral sites. Podowski *et al.* (2010) showed that *Austinograea* spp. prefer the higher temperature diffuse flow habitats in the Lau Basin, and our study revealed that these animals, along with shrimp, were found in much lower numbers at peripheral sites compared to areas of active venting.

Although certain species commonly associated with areas of robust diffuse flow such as *Branchinotogluma segonzaci* polynoids, paralvinellid worms and *Alviniconcha* snails were absent from the peripheral sites, most other species found associated with active venting were also present at the peripheral assessment sites. Additionally, these peripheral communities host non-vent taxa such as sponges, corals and seastars, which roughly balance the number of vent-endemic taxa not present, resulting in very similar values for overall taxonomic richness among the different habitats.

Although they do not host nearly the biomass present on edifices or in more active diffuse flow, peripheral communities tend to host higher biomasses and densities of background fauna than the surrounding deep sea (Lonsdale 1977; Arquit 1990; Galkin 1997). This was also evident in this study of Lau Basin communities, and in fact, peripheral sites were chosen for this study based on visibly higher concentrations of megafauna. Practical constraints precluded the random selection of study sites in this rugged environment and lack of data on animal and diffuse flow distribution on the scale of a vent field preclude evaluation of patterns of species presence and abundances as a function of increasing distance from sources of active venting, as suggested by Kim & Hammerstrom (2012). Our methodology was designed to compare patterns of community composition along a north–south gradient, test for correlations with changes in chemistry along that gradient, and examine temporal changes in the Lau Basin peripheral communities over a 3-year period.

Peripheral vent communities represent a transition zone between very high biomass communities that form in areas of robust diffuse hydrothermal flow and the regular deep-sea benthic community that derives its nutrition from photosynthetic sources. The most abundant and visually obvious members of the peripheral communities are all likely carnivorous. *Abyssocladia dominalba* and *Asbestopluma* sp. are both cladorhizid sponges, a family that is known to be largely carnivorous (Vacelet & Boury-Esnault 1995; Vacelet 2007). Similarly the cnidarians are all very likely carnivorous, as theoretical considerations suggest that chemoautotrophic symbioses are unlikely in this group (Childress & Girguis 2011), and most cnidarians that do not contain autotrophic symbionts are carnivores. Small zooplankton feeding on vent primary productivity would be likely conduits for vent primary productivity to these peripheral communities. In addition, several authors have suggested that active hydrothermal venting can increase local supply of particulate organic carbon by concentrating both locally produced and photosynthetically produced particulates in advection cells (Lonsdale 1977; Enright *et al.* 1981; Galkin 1997).

Temporal change in peripheral communities and comparison to temporal trends in near-vent communities

The patterns of change in the communities over the 3 years of this study can be divided into two overlapping categories, as was found in more active areas of Lau Basin vent fields (Sen *et al.* 2014). The most common is no significant changes in the composition or structure of the communities albeit with changes in the abundance of some faunal groups. This is likely related to either undetectable or minor changes in the composition of the emitted hydrothermal fluid. KM2P, ABE1P, ABE2P and TM1P fall within this category; at all these sites, most of the temperature measurements taken were above ambient temperatures in both years of sampling. At the latter three assessment sites, there were no detectable differences in the sulfide composition of the venting fluid as sulfide was not detected at these sites in either 2006 or 2009. At KM2P, sulfide was not detected in 2006, but in 2009, sulfide was detected at 15 locations, although at very low levels. Based on a composite data set of ~20,000 electro-chemical scans taken on the ELSC-VFR in 2006 and 2009, Luther *et al.* (2012) found an overall increase in the sulfide-to-temperature ratio over time at all the vent fields with the exception of Tu'i Malila. Gartman *et al.* (2011) and Sen *et al.* (2014) found the same trend for measurements taken at active vent sites. Therefore, the low levels of sulfide measured at KM2P in 2009 do not necessarily reflect major changes in the local plumbing, but rather may be a reflection of widespread temporal changes in the fluid composition noted all across the ELSC-VFR. This result is similar to what Sen *et al.* (2014) reported in areas of active venting, where communities exhibited minor and non-significant changes in community composition when fluid regimes did not undergo significant changes in chemistry or magnitude of fluid flow over time.

A second pattern observed in both near-vent and peripheral communities was likely related to a significant decline in venting. Like KM1 in Sen *et al.* (2014), KM1P experienced a dramatic decline in venting and had the highest Wilson–Shmida beta diversity and the lowest similarity indices between the years of study. These two sites are only 4 m apart from one another and the cessation of venting at both is very likely related to the same subsurface event. KM1 in 2009 was more similar to peripheral communities (Fig. 5) than to other active vent communities, indicating that peripheral communities may represent a late successional stage of active communities, as well as potentially arising *de novo* in areas with very limited, but near-field venting.

Anemones decreased in numbers across all peripheral assessment sites between visits. Their numbers also decreased substantially over time at the KM1 active vent site concomitant with the dramatic decrease in activity at that site (Sen *et al.* 2014). Podowski *et al.* (2010) found that anemones in the ELSC-VFR are found in conditions that are significantly different from ambient (although oxygen is near ambient, sulfide concentrations do not exceed 19 $\mu mol \cdot l^{-1}$ and temperatures do not exceed 9 °C) and concluded that these anemones can tolerate a small amount of hydrothermal venting and probably benefit from the higher primary productivity associated with these areas. Our results support this conclusion and we suggest that these anemones require the higher levels of local primary productivity and may also benefit from reduced predation in this environment. Anemones can be quite mobile (Mcclendon 1906; Parker 1916, 1917; Hyman 1940; Dunn 1976) but are also capable of remaining in one location for extended periods of time when oxygen and food are in abundant supply (Osburn 1914). Their relative immobility as adults reported here may be an adaptation to capitalize on the limited number of favorable locations within their habitat.

Polynoid–anemone association

Three species of polynoid polychaetes were present in the peripheral communities in the KM vent field, where anemones were also abundant. Two of the species present, *Branchinotogluma* sp. nov. and *Levensteiniella raisae*, were found on or in very close proximity to anemones more often than predicted by chance alone. The third, a species in the subfamily Harmothoinae, did not show a preference for association with anemones. Polynoids associated with anemones with fully extended tentacles would not be visible in our down-looking photographs and so we very likely underestimated polynoids associated with anemones.

It is possible that anemone-associated polaggerynoids simply prefer habitat structure or protected locations. However, neither the anemone-associated nor non-associated polynoids were observed near rocks or biotic substrate similar in size to anemones. A complicating factor is that the polynoids were seen only in the northern sites where the substrate tends to be smooth pillow basalts and smaller rocks are uncommon; thus, we could not directly test the hypothesis of structure association.

Polynoids are well known for their symbiotic associations and in fact, more than half (55%) of all known commensal polychaetes are polynoids (Martin & Britayev 1998). Polynoid–cnidarian associations are common and have been reported with hydroids (Di Camillo *et al.* 2010), gorgonians (Pettibone 1991a), antipatharians (Pettibone 1991b) and even a species of unattached coral (Pettibone 1989). Pettibone (1963) described an association between a polynoid, *Alentiana aurantiaca*, and an actinarian anemone, *Bolocera tuediae*. The worm was seen among the tentacles of the anemone and it was described as being a facultative relationship. However, in the Lau sites, we did not see any polynoids among the tentacles of anemones. Instead, the polynoids were seen near or on the bases of anemones. It is not known whether or how either partner benefits from the relationship; however, the Lau polynoids match their hosts' coloration, which is common among polynoids in a trophic symbiosis (Gibbs 1969; Pettibone 1993; Martin & Britayev 1998; Di Camillo *et al.* 2010) as well as those thought to associate with hosts for protection from predation (Pettibone 1991b; Martin & Britayev 1998). The Harmothoinae polynoids that were not seen to associate with anemones tend to have a darker, yellowish color, which did not match the white coloration of the anemones and anemone-associated polynoids.

Cladorhizid sponge life history strategies

The populations of cladorhizid stick sponges *Asbestopluma* sp. were surprisingly dynamic in the peripheral sites. Although demosponges are commonly considered to be slow-growing and long-lived species (Garrabou & Zabala 2001), these cladorhizids appear to have a very different lifestyle. Numbers of individuals declined at the two sites with abundant stick sponges and sufficient image quality to confidently identify the individuals present. At ABE1P much of the vent field was poorly illuminated in 2006; however, numerous individuals clearly visible in 2006 were gone in 2009. Furthermore, we also clearly observed significant growth in several individuals of *Asbestopluma* sp. (Fig. 5). Cladorhizid sponges are unique among Porifera in that they lack an aquiferous filtering system and capture small motile animals such as crustaceans for food (Vacelet & Boury-Esnault 1995). One species has even been discovered that has symbiotic methanotrophic bacteria (Vacelet *et al.* 1996). The unique feeding habits of cladorhizid sponges are considered to be adaptations for survival in the food-poor habitat of the deep sea (Vacelet & Boury-Esnault 1995; Vacelet 2007). Cladorhizid sponges are considered 'sit and wait' predators and expend very little energy between feeding opportunities (Vacelet 2007). This strategy, combined with a higher food supply rate in peripheral communities compared to the surrounding deep sea, could contribute to relatively fast growth rates for some individuals, and reliance on above-average but ephemeral food availability may explain the relatively high mortality rates within the population. Interestingly, we did not detect any growth or mortality among the individuals of the other cladorhizid sponge observed in this study, *Abyssocladia dominalba*. It was previously reported from tops of inactive chimneys (Desbruyères *et al.* 2006). The small size of this species is typical of cladorhizid sponges (Hajdu & Vacelet

2002) and may contribute to its stability in the face of waning hydrothermal activity.

Conclusions

Peripheral communities exhibit many of the trends observed in near-vent communities, such as a shift in community composition along the length of the Lau Basin and two major temporal patterns: overall stability over 3 years, albeit with minor differences in faunal abundances, when fluid chemistry and flow did not exhibit large changes, and large-scale community changes when the fluid regime changed substantially. Peripheral communities can be temporally and spatially separated from areas of active diffuse venting, and host both vent endemic and non-vent endemic fauna. Peripheral communities host similar numbers of species as near-vent communities, but the relative abundance of carnivorous suspension feeders could make these communities particularly susceptible to the suspended debris resulting from deep-sea mining. Furthermore, peripheral communities could be connected to near-vent communities in ways not yet studied in the Western Pacific, such as serving as brooding or nursery grounds for vent endemic species (Epifanio *et al.* 1999; Dittel *et al.* 2008). Therefore, focusing mining activity in peripheral regions could lead to limited recruitment of species at hydrothermal vents in addition to mortality of benthic species that populate the surrounding areas. All of these factors must be considered as mining policies and regulations are drafted.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map of the Kilo Moana vent field.

Figure S2. Map of the Tow Cam vent field.

Figure S3. Map of the ABE vent field.

Figure S4. Map of the Tu'i Malila vent field.