



Biotic and abiotic factors affecting distributions of megafauna in diffuse flow on andesite and basalt along the Eastern Lau Spreading Center, Tonga

Elizabeth L. Podowski¹, Shufen Ma^{3,4}, George W. Luther III³, Denice Wardrop², Charles R. Fisher^{1,*}

¹Biology Department and ²Geography Department, Pennsylvania State University, University Park, Pennsylvania 16802, USA

³College of Marine and Earth Studies, University of Delaware, Lewes, Delaware 19958, USA

⁴Present address: Department of Earth and Planetary Sciences, University of California, Berkeley, California 94720, USA

ABSTRACT: Imagery and environmental data from 7 diffuse flow hydrothermal vent sites along the Eastern Lau Spreading Center (ELSC) are used to constrain the effects of lava type, temperature, chemistry, and biological interactions on faunal distributions. Of the species with chemoautotrophic endosymbionts, the snail *Alviniconcha* spp. occupies habitats with the greatest exposure to vent fluids. Temperatures exceeding 45°C define its upper limit of exposure to vent flow, and minimum sulfide requirements constrain its lower limits. The mussel *Bathymodiolus brevior* experiences the least exposure to vent flow; temperatures of about 20°C determine its upper limit, while its lower limit is defined by its minimum sulfide requirements. The snail *Ifremeria nautilei* inhabits areas with intermediate exposure to vent fluids and biological interactions are likely the most important factor shaping this snail's realized niche. Microhabitats of non-symbiont-containing fauna were defined in terms of symbiont-containing faunal distributions. The crab *Austinograea* spp. occupies areas with the greatest exposure to vent flow; shrimp, the snail *Eosipho desbruyeresi*, and anemones inhabit intermediate zones of vent flow; and the squat lobster *Munidopsis lauensis* dominates the periphery of diffuse flow areas, with little exposure to vent fluids. The physical structure of different lava types along the ELSC differentially affects the diffusion of vent fluids, which has a variety of implications for fauna, particularly distributions of zoanths, anemones, and mixed communities of *I. nautilei* and *B. brevior*.

KEY WORDS: Lau back-arc basin · Faunal distributions · Diffuse flow · Lava type · *In situ* voltammetry · GIS

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The 400 km-long Eastern Lau Spreading Center (ELSC) is located in the Lau back-arc basin, bordered on the west by the remnant Lau arc and on the east by the active Tofua volcanic arc and the Kingdom of Tonga (Parson et al. 1990, Taylor et al. 1996). The northernmost segment of the ELSC is 110 km from the active arc, while the southernmost segment (the Valu Fa Ridge) is separated from the volcanic arc by only 40 km (Martinez et al. 2006). As a result of variable

proximity to a subduction zone, geophysical processes and geochemical properties change systematically along a north to south gradient. For example, magmatic robustness (Martinez & Taylor 2002, Martinez et al. 2006) and crustal thickness (Martinez & Taylor 2002, Taylor & Martinez 2003) increase from north to south, while spreading rate (Martinez & Taylor 2002), plume incidence (Martinez et al. 2006), concentrations of dissolved H₂ and H₂S in end-member vent fluids (Seewald et al. 2005), and depth all decrease. Lava type also changes along a north to south gradient: the

northern portion of the ELSC is basalt-hosted and the southern portion is andesite-hosted (Vallier et al. 1991). Andesitic lavas have a higher silica content than basaltic lavas (Press & Siever 1974), and as a result of hydrous melting, andesitic lavas in the Lau Basin tend to be more permeable (Hawkins 1995) and vesicular (Vallier et al. 1991) compared to more basaltic lavas.

The ultimate source of energy for primary production at hydrothermal vents is derived from reduced chemicals (particularly sulfide) in vent effluent, which can also be toxic and hot. As a result, the vent environment is fundamentally different from most other environments because primary production is usually positively correlated with environmental stress. Gradients of environmental change are also very steep in areas of hydrothermal diffuse flow, where vent effluent mixes with the surrounding seawater, and can vary on scales of centimeters and seconds. Thus in a vent community, tolerance of extremes in chemistry and temperature may be a first order determinant of a species' ability to make use of the primary production associated with these habitats. However, biological interactions will play an important role in defining patterns of animal distribution in areas where abiotic factors are less extreme. Understanding the relation between different animals and the abiotic environment and the role of biological interactions in structuring the vent communities have been a primary focus of ecological research at vents for 2 decades. Our understanding of the factors affecting hydrothermal vent community structure has been significantly advanced as a result of intensive research efforts on the Mid-Atlantic Ridge (Desbruyères et al. 2000, 2001), the East Pacific Rise (Hessler et al. 1985, 1988, Fisher et al. 1994, Johnson et al. 1994, Shank et al. 1998, Luther et al. 2001, Van Dover 2003), and the Juan de Fuca Ridge (Sarrazin & Juniper 1999, Sarrazin et al. 1999, Govenar et al. 2002, Bergquist et al. 2007); however, relatively few studies have focused on vent communities in the Western Pacific, particularly the ELSC (Desbruyères et al. 1994, Podowski et al. 2009). The mobility of the symbiont-containing fauna in this biogeographic province holds promise for new insights into the fundamental processes that structure vent animal communities.

The natural abiotic variation along the ELSC provides a unique opportunity to examine how chemistry and lava type affect local hydrothermal vent communities. The diffuse flow vent fields in the ELSC host high biomass communities (Desbruyères et al. 1994), similar in composition to other back-arc basins in the Western Pacific (Tunnicliffe & Fowler 1996, Van Dover et al. 2002). These vent communities are dominated in biomass by provannid snails *Alviniconcha*

spp. (3 different species, including *Alviniconcha hessleri* [Okutani & Ohta 1988], that are not differentiable in images) and *Ifremeria nautilei* (Bouchet & Warén 1991), and the bathymodiolin mussel *Bathymodiolus brevior* (von Cosel et al. 1994), all of which require exposure to hydrothermal vent fluids in order to maintain nutritional symbioses with chemoautotrophic microbes housed in their gills (Endow & Ohta 1989, Windoffer & Giere 1997, Dubilier et al. 1998, Suzuki et al. 2005a, Urakawa et al. 2005). Unlike the vestimentiferan tubeworms that dominate many diffuse flow vents on the East Pacific mid-ocean ridges, the symbiont-containing snails and mussels of the ELSC are mobile, an adaptation that enables each species to respond to local changes in hydrothermal flow and seek the most suitable habitat available. Previous studies (Desbruyères et al. 1994, Podowski et al. 2009) have documented the distributional patterns and generally defined the microhabitats of the abovementioned ELSC species. Aggregations of *Alviniconcha* spp. are found in high-temperature and sulfide-rich environments (Desbruyères et al. 1994, Podowski et al. 2009). *I. nautilei* occur in a fairly wide range of intermediate chemical and thermal environments (Podowski et al. 2009) and *B. brevior* are found in environments with the least exposure to vent fluids (Podowski et al. 2009). Both *Alviniconcha* spp. and *I. nautilei* occur as 2 different color morphotypes that can be distinguished in the mosaics. Prior to this study, it was not known whether the distribution of the different color morphotypes was correlated with differences in microhabitats.

In this study, we used new data sets collected from 7 diffuse flow communities distributed among 4 vent fields and across 2 lava types to test hypotheses from previous studies and further define the relationships between chemistry, lava type, and biology along the ELSC. Ratios of sulfide concentration to temperature anomaly (i.e. degrees above ambient temperature) vary significantly among sites, enabling us to partially separate the relative importance of these typically confounded parameters and test the hypotheses from Podowski et al. (2009) that temperature determines the upper limits of vent exposure for *Alviniconcha* spp. and *Bathymodiolus brevior*, while sulfide concentration determines the upper limit of exposure of *Ifremeria nautilei* to vent fluid. Furthermore, this larger data set enabled statistical examination of the distributional patterns of other common back-arc basin vent megafauna and the detection of differences in community composition on andesitic and basaltic lavas, including the examination of how different lava types disperse hydrothermal fluid, which may explain in part the observed differences between communities on the 2 lava types.

MATERIALS AND METHODS

In situ imagery. The study was carried out in four vent fields along the ELSC, known as Kilo Moana (KM), Tow Cam (TC), ABE, and Tui Malila (TM) (Fig. 1). A total of 7 diffuse flow communities (assessment sites) were imaged and surveyed chemically and thermally in September 2006 (Table 1). Sites with symbiont-containing fauna (indicative of diffuse flow) that were relatively flat and could be accessed by the submersible were chosen for study. Two of the assessment sites were established and surveyed in 2005 (ABE1 and TM1; Podowski et al. 2009), 3 were established but not chemically surveyed in 2005 (KM1, containing marker 29, TC1, containing marker 31, and ABE2, containing marker 32), and the 2 others were established in 2006 (KM2, containing markers 55 and 56, and TC2, containing markers 64 and J).

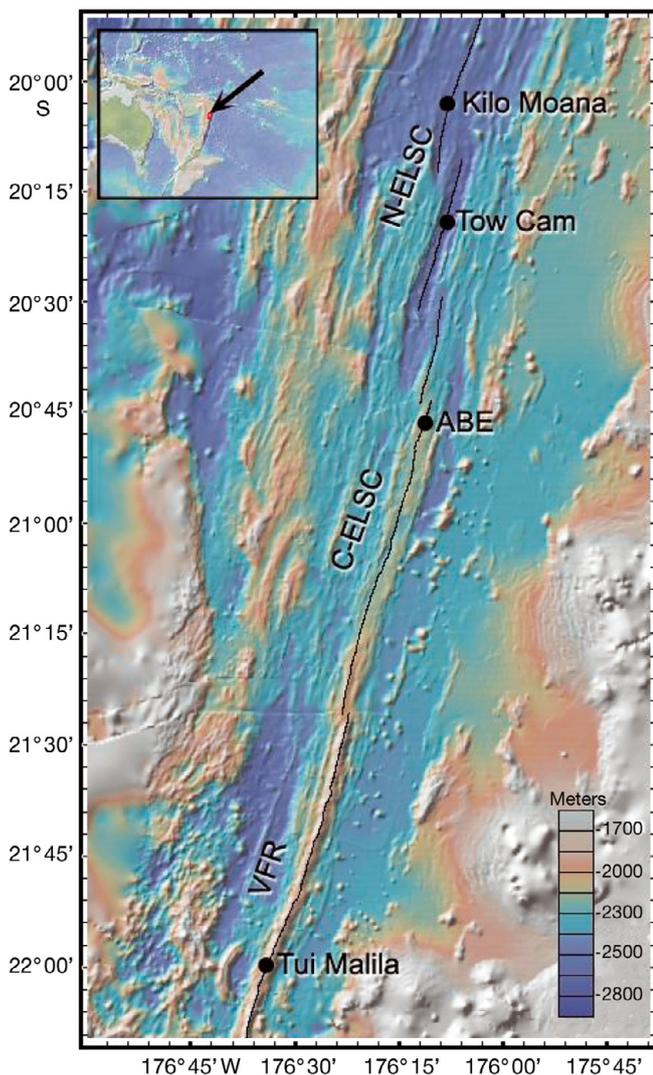


Fig. 1. Locations of the 4 major vent fields surveyed along the Eastern Lau Spreading Center in 2006. Map courtesy of V. Ferrini (Ferrini et al. 2008, Ryan et al. 2009)

Each assessment site was imaged twice using the remotely operated vehicle (ROV) 'Jason II'. One set of images was collected from 2 m above the seafloor and 2 sets were collected simultaneously using 2 different down-looking camera systems from 5 m above the seafloor. A high-dynamic-range, color, digital camera (Habcam system) was used to obtain lower resolution images from an altitude of 5 m that were downloaded in real time from the ROV. These Habcam system images were immediately optimized in Photoshop, mosaicked together using a customized MatLab program (Pizarro & Singh 2003, V. Ferrini pers. comm.), printed, and used to guide chemical and temperature measurements when the site was revisited later during the same dive. A Nikon Coolpix Insite Scorpio digital camera system was used to obtain high-resolution imagery of the assessment sites from each altitude. Images from 5 m were used to construct final mosaics of each assessment site and the higher resolution images obtained at an altitude of 2 m were hyperlinked within a GIS and used for species identifications (Podowski et al. 2009). Due to time and basket loading constraints on 2 dives, KM2 and TC2 were only imaged once at an intermediate altitude of 3 m (KM2 with the Nikon Coolpix and TC2 with the Habcam). This provided images of manageable file size to produce mosaics and sufficient resolution for species identifications.

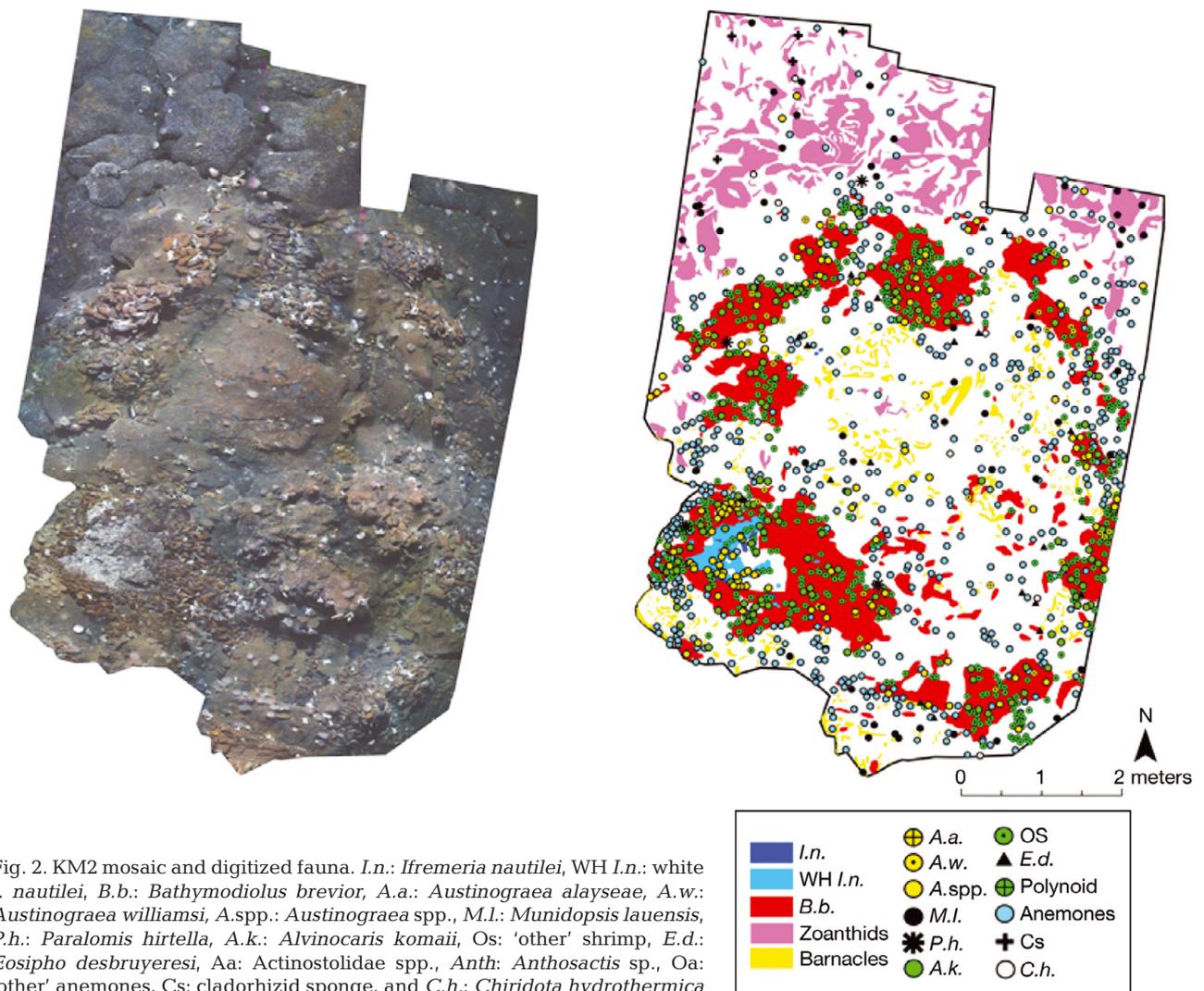
Digitization of fauna. Mosaics from each assessment site were imported into ArcView 9.0, geo-referenced in the WGS 1984 UTM Zone 1S coordinate system, and all images were hyperlinked to the mosaic (Podowski et al. 2009). The 2 m high-resolution imagery was referenced to digitize cover of aggregated fauna and distributions of solitary fauna (Fig. 2 and the supplement at www.int-res.com/articles/suppl/m418p025_supp.pdf). Aggregated fauna (including symbiont-containing and attached fauna) were digitized as separate polygon layers and the solitary fauna (other megafauna) as separate point layers. The categories of aggregated fauna digitized separately included: *Alviniconcha* spp. with light and dark shells (white, dark, and mixed white and dark aggregations), *Ifremeria nautilei* with light and dark shells (white, dark, and mixed aggregations), *Bathymodiolus brevior*, mixed communities of *I. nautilei* & *B. brevior*, barnacles (the 3 known orders of sessile barnacles in the Lau Basin could not be differentiated in the images and were grouped into one category), zoanths, and mixed aggregations of zoanths and barnacles. Solitary faunal categories included: the brachyuran crabs *Austinograea alayseae*, *Austinograea williamsi*, and *Austinograea* spp. (when the 2 species could not be differentiated), the anomuran crabs *Munidopsis lauensis* and *Paralomis hirtella*, the shrimp *Alvinocaris komaii* (the only shrimp large and

Table 1. Characteristics of the 7 assessment sites

Site	Location	Depth (m)	Dominant lava type	Area mosaicked (m ²)	Species richness (n)
KM1	20°3'9.6" S, 176°8'1.9" W	2615	Basalt	21.9	15
KM2	20°3'13.7" S, 176°8'1.0" W	2618	Basalt	45.2	15
TC1	20°19'0.0" S, 176°8'10.3" W	2705	Basalt	33.7	14
TC2	20°18'58.8" S, 176°8'11.3" W	2720	Basalt	14.5	7
ABE1	20°45'47.3" S, 176°11'29.1" W	2140	Andesite	41.8	14
ABE2	20°45'40.7" S, 176°11'25.3" W	2140	Andesite	5.5	13
TM1	21°59'20.7" S, 176°34'5.8" W	1890	Andesite	32.1	12

distinctive enough to be regularly differentiated in the images), 'other' shrimp (*Alvinocaris komaii*, *Lebbeus* sp., *Chorocaris vandoverae*, and *Nautilocaris saintlaurentae*), the stalked barnacle *Vulcanolepas* sp., the snails *Eosipho desbruyeresi* and *Phymorhynchus* sp., polynoids (*Harmothoe* sp. and *Levensteiniella* sp.; the 2 species could not be distinguished), anemones (this category includes predominantly *Cyananthea hour-*

dezi and *Actinostolidae* sp. and at least one individual of *Alvinactis chessi*; however, the 3 species could not be reliably differentiated), cladorhizid sponges, the holothurian *Chiridota hydrothermica*, and the fishes *Thermarces* sp. and *Thermobiotes mytilogeiton*. Percent cover of aggregated fauna and densities of solitary fauna were calculated based on the total area of each assessment site (see Table 3).



***In situ* chemical and thermal measurements.** *In situ* voltammetry was used to document the concentrations of free sulfide and oxygen at 31 to 100 points (survey locations) within each assessment site (Luther et al. 2001, Nuzzio et al. 2002, Podowski et al. 2009). The minimum detectable and quantifiable concentration of sulfide was $0.2 \mu\text{mol l}^{-1}$. Undetectable sulfide measurements were treated as $0.1 \mu\text{mol l}^{-1}$ (half of the detection limit) for statistical purposes. We used a conservative detection limit of $5 \mu\text{mol l}^{-1}$ and a quantification limit of $15 \mu\text{mol l}^{-1}$ for oxygen concentration. Oxygen could be detected between concentrations of 5 and $15 \mu\text{mol l}^{-1}$, but could not be quantified as a result of noise from the ROV and variable overlap with high sulfide current signals. For statistical analyses, $2.5 \mu\text{mol l}^{-1}$ (half of the detection limit) was used for all undetectable oxygen concentrations and $10 \mu\text{mol l}^{-1}$ (average of quantification and detection limits) was used for all non-quantifiable oxygen concentrations.

The number of survey locations within an assessment site reflected the size of the assessment site and the diversity of megafauna present. Survey locations were chosen in order to characterize a representative subset of visible microhabitats within the assessment site, spread over as large an area as possible. The survey locations chosen were sometimes limited by the ability of the ROV to access the location or our ability to recognize the location on the mosaic print-out at the time of the survey. At each survey location, the electrochemical wand housing the working electrodes and a thermistor was placed over the point of interest and the precise location was recorded on a hard copy of the low-resolution mosaic of the assessment site. In order to test the hypothesis that

symbiont-containing species are consuming sulfide and potentially altering the chemistry of their surrounding environment, a subset of the measurements taken over aggregations of animals was paired to measurements taken directly under the same point at 5 assessment sites (KM2, number of paired measurements $n = 16$; TC1, $n = 5$; ABE1, $n = 14$; ABE2, $n = 7$; and TM1, $n = 19$). The 'under' measurement was taken immediately following the 'over' measurement by pushing the electrochemical wand down through the aggregation to the seafloor.

At each survey location a set of 7 to 10 electrochemical scans were taken, each lasting approximately 8 s (Podowski et al. 2009). Temperature measurements were recorded immediately prior to each electrochemical scan. Maximum, minimum, average, and median temperature and sulfide and oxygen concentrations were recorded for each survey location. The number of survey locations scanned in each assessment site is displayed in Table 2.

In addition to chemical and temperature measurements using the electrochemical wand, a majority of the assessment sites (KM2, TC1, ABE1, ABE2, and TM1) were revisited within 10 d and temperature measurements were taken at additional locations using the JASON II high-temperature probe. Maximum and minimum temperatures were recorded at each of these thermal survey locations and average values calculated. The thermistor housed in the electrochemical wand was cross-calibrated to the JASON II high-temperature probe during 2 descents through the water column. The number of additional temperature measurements in each assessment site is shown in Table 2.

Table 2. Environmental characteristics of each assessment site. Ambient O_2 values were obtained from Niskin water samples while transiting between diffuse flow communities in ambient water. Data for max. H_2S , min. O_2 and max. T show the range of values recorded at each site followed by the median value in parentheses, skewness (italicized) and kurtosis (italicized). Values for slope of H_2S vs. temp anomaly are followed by R^2 values in parentheses. UD = undetectable

Site	Ambient temp. ($^{\circ}\text{C}$)	Ambient O_2 (μM)	Chem. & temp. locations (n)	Temp. only locations (n)	Max. H_2S (μM)	Min. O_2 (μM)	Max. temp. ($^{\circ}\text{C}$)	Slope of H_2S vs. temp. anomaly
KM1	2.3	168	31	0	UD-190 (UD) <i>5.4, 29.7</i>	UD-146 (120) <i>-1.8, 2.1</i>	2.5-18.0 (4.5) <i>2.5, 5.7</i>	6.9 (0.53)
KM2	2.3	168	69	59	UD-132 (10) <i>2.9, 8.4</i>	UD-163 (75) <i>0.0, -1.4</i>	2.5-17.7 (4.1) <i>1.7, 2.8</i>	5.5 (0.61)
TC1	2.4	174	71	38	1-165 (9) <i>2.0, 2.8</i>	UD-137 (103) <i>-0.9, -0.8</i>	2.5-32.5 (4.5) <i>1.9, 3.1</i>	5.3 (0.74)
TC2	2.4	174	48	0	2-190 (13) <i>3.3, 14.0</i>	UD-97 (60) <i>-0.4, -1.5</i>	2.5-24.5 (5.5) <i>2.7, 9.9</i>	7.7 (0.84)
ABE1	2.4	175	101	94	1-166 (15) <i>2.3, 5.5</i>	UD-180 (119) <i>-0.5, -1.3</i>	2.9-78.1 (7.5) <i>2.9, 12.6</i>	3.3 (0.58)
ABE2	2.4	175	35	24	UD-27 (1) <i>1.5, 1.2</i>	10-139 (91) <i>-0.4, -1.5</i>	2.5-20.4 (4.5) <i>1.5, 1.5</i>	1.4 (0.63)
TM1	2.5	169	81	44	UD-130 (4) <i>3.4, 12.4</i>	UD-24 (74) <i>-0.5, -0.9</i>	2.8-42.4 (6.9) <i>1.8, 3.3</i>	1.8 (0.47)

Analyses of chemical/thermal environments of aggregated and attached fauna. Multiple Mann-Whitney pairwise comparisons were performed to determine whether there were significant differences in the average chemical (sulfide or oxygen concentrations) or thermal environments (average temperature anomaly) experienced by the different aggregated faunal categories (Minitab version 12.21, 1998). The chemical/thermal environments inhabited by white and dark *Alviniconcha* spp. were compared (9 total comparisons among homogenous white, homogenous dark, and mixed white and dark categories), the chemical/thermal environments of white and dark *Ifremeria nautilei* were compared (3 total comparisons between homogenous white and homogenous dark categories), and the chemical/thermal environments of mixed aggregations of *I. nautilei* and *Bathymodiolus brevior*, homogenous aggregations of *I. nautilei* (white, dark and mixed *I. nautilei* were combined), and homogenous aggregations of *B. brevior* were compared (9 total comparisons). All categories within a given species were combined to compare the chemical/thermal environments inhabited by the different aggregated faunal types (30 total comparisons): *Alviniconcha* spp. (including the white and dark categories), *I. nautilei* (including the white, dark, and mixed with *B. brevior* categories), *B. brevior* (including solitary and mixed with *I. nautilei* categories), barnacles, and zoanthids. Appropriate significance levels for all comparisons were determined using a sequential Bonferroni correction.

In order to examine sulfide consumption by faunal aggregations, the ratio of total sulfide concentration to temperature anomaly over the fauna was calculated and compared to that in a paired measurement taken under the fauna (Table 2). If symbiont-containing fauna are consuming sulfide, we expect the ratio of sulfide to temperature anomaly to be significantly greater under fauna than over. Mann-Whitney pairwise comparisons were used to test for differences within the entire data set and then within various subsets of the data set (data were grouped by vent field and also by species).

Analyses of community composition across lava types. Two Bray-Curtis similarity matrices were generated for each assessment site using relative cover of aggregated fauna (after an arcsine square root transformation all data sets were normally distributed) and density of solitary fauna (after a square root transformation all data sets but polynoids were normally distributed). For this analysis, the solitary faunal matrix combined categories of taxa that could not consistently be differentiated. For example, the density of austinograeaid crabs was calculated by combining *Austinograea alayseae*, *A. williamsi*, and *Austinograea* spp.

The same was done with shrimp (*Alvinocaris komaii* and 'other' shrimp were combined into one category). Average linkage clustering was used to determine similarity of community composition between assessment sites (PRIMER version 5.2.9, 2002), and analyses of similarity (ANOSIM) were run in PRIMER using the Bray-Curtis similarity matrices with lava type as the factor. The effect of lava type and venting field (nested within lava type) on each type of aggregated and solitary fauna was tested using a general linear model (Johnson & Wichern 2007; Minitab version 12.21, 1998).

Six isotropic variograms were constructed (Gamma Design Software, GS+ 2007) in order to analyze the spatial autocorrelation of each abiotic variable measured (temperature, sulfide, and oxygen) on the 2 different lava types (basalt and andesite). Semivariance was calculated using the equation:

$$\gamma(h) = [1 / 2N(h)] \sum (z_i - z_{i+h})^2$$

where $\gamma(h)$ is the semivariance for the interval distance class (lag interval) h , z_i is the value of the measured sample at point i , z_{i+h} is the value of the measured sample at point $i + h$, and $N(h)$ is the total number of sample pairs in the lag interval h (Wackernagel 1995). Within each lag interval, the semivariance for that group of measurements was calculated and plotted and a spherical isotropic model was fitted to each variogram. Different distance intervals (h) were tested, ranging from 5 cm to 25 cm, until an interval size was found that maximized the variance explained by the spherical model. A total distance of 2 m (lag distance), divided into 10-cm lag intervals, was analyzed in all 6 variograms. Constant semivariance across each lag interval (zero slope) indicates that there is no spatial structure in the data, while changing semivariance across lag intervals indicates spatial structure (Wackernagel 1995). The distance at which pairs of measurements of a particular variable are no longer autocorrelated is referred to as the range, and the sill is the semivariance value at which the variogram reaches an asymptote (Wackernagel 1995). The semivariance at $h = 0$ is referred to as the nugget variance. A nugget variance of zero indicates that all of the spatial variability of a particular variable was captured with the sampling scale employed. Nugget values greater than zero and approaching the sill value are likely a result of error associated with the *in situ* measurements, random variability, and/or the use of a scale not fine enough to capture all variability (Corstanje et al. 2006).

Distribution of solitary faunal species. A GIS location-based query provided information on how solitary fauna were distributed across different substratum types (including each aggregated faunal category and bare substrata). For every species of solitary fauna with

a population of ≥ 5 individuals, χ^2 analyses were performed to test the null hypothesis that solitary fauna were randomly distributed across all substratum types. All symbiont-containing fauna require exposure to vent flow. The presence of other fauna directly on symbiont-containing species indicates a tolerance for the same environmental conditions to which the symbiont-containing fauna are exposed. In order to identify fauna that maintain a close proximity to vent flow while avoiding direct exposure, we analyzed distributions of solitary fauna within 5 cm of symbiont-containing fauna. For this analysis, all polygons representing *Alviniconcha* spp., *Ifremeria nautiliei*, and *Bathymodiolus brevior* were merged into a single polygon type, around which a 5 cm buffer was generated.

RESULTS

Sulfide consumption by symbiont-containing faunal aggregations

Ratios of sulfide to temperature anomaly were significantly greater under aggregations of symbiont-containing fauna compared to over aggregations ($W = 3536$, $df = 1$, $n = 56$, $p < 0.02$). This is consistent with laboratory studies that confirmed these species con-

sume sulfide (Henry et al. 2008) and indicates that the symbiont-containing fauna can alter the chemistry of their immediate microhabitat. Partitioning the data set by species or by vent field resulted in relatively small data sets and no significant differences were detected in these subsets of the data.

Chemical/thermal environment of aggregated and attached fauna

Alviniconcha spp. were present in all but 2 assessment sites (Table 3) and were the dominant symbiont-containing species present in TC2, covering 10% of the assessment area. Average temperature anomalies among *Alviniconcha* spp. ranged from 0.1 to 38.5°C, and the highest temperature measured was 42.4°C. Average sulfide concentrations detected among these species ranged from undetectable to 142 $\mu\text{mol l}^{-1}$, and the highest sulfide concentration measured was 190 $\mu\text{mol l}^{-1}$. Average oxygen concentrations ranged from undetectable to 169 $\mu\text{mol l}^{-1}$. Sulfide concentrations and temperatures measured among *Alviniconcha* spp. were significantly higher and oxygen concentrations significantly lower than those measured among all other species in the aggregated faunal category (Fig. 3).

Table 3. Percent cover of aggregated fauna and abundance (n) and density (n m^{-2}) of solitary faunal species observed in each assessment site. See Table 1 for area mosaicked at each assessment site

Species	KM1	KM2	TC1	TC2	ABE1	ABE2	TM1
Aggregated fauna (%)							
<i>Alviniconcha</i> spp.	<1	–	<1	10	5	–	5
<i>Ifremeria nautiliei</i>	1	1	13	<1	15	9	9
Mixed <i>I. nautiliei</i> & <i>Bathymodiolus brevior</i>	<1	–	1	–	6	15	2
<i>Bathymodiolus brevior</i>	13	20	11	–	6	9	2
Barnacles	2	2	3	3	6	2	<1
Zoanthids	2	8	9	–	–	–	–
Solitary fauna, n (n m^{-2})							
<i>Thermarces</i> sp.	2 (0.1)	–	–	–	1 (0.0)	1 (0.2)	–
<i>Thermobiotus mytilogeiton</i>	–	–	–	–	7 (0.2)	1 (0.2)	–
<i>Chiridota hydrothermica</i>	9 (0.4)	13 (0.3)	13 (0.4)	–	–	–	–
<i>Austinograea</i> spp.	74 (3.4)	118 (2.6)	93 (2.8)	32 (2.2)	139 (3.3)	15 (2.7)	87 (2.7)
<i>Austinograea alayseae</i>	–	4 (0.1)	1 (0.0)	–	16 (0.4)	5 (0.9)	7 (0.2)
<i>Austinograea williamsi</i>	5 (0.2)	35 (0.8)	7 (0.2)	–	17 (0.4)	2 (0.4)	2 (0.1)
<i>Munidopsis lauensis</i>	31 (1.4)	49 (1.1)	76 (2.3)	2 (0.1)	504 (12.1)	50 (9.1)	137 (4.3)
<i>Paralomis hirtella</i>	1 (0.1)	4 (0.1)	–	–	16 (0.4)	1 (0.2)	–
<i>Alvinocaris komaii</i>	18 (0.8)	152 (3.4)	15 (0.4)	–	58 (1.4)	–	–
Other shrimp	15 (0.7)	468 (10.4)	121 (3.6)	2 (0.1)	300 (7.2)	3 (0.5)	141 (4.4)
<i>Vulcanolepas</i> sp.	–	–	15 (0.4)	–	–	–	–
<i>Eosipho desbruyeresi</i>	8 (0.4)	20 (0.4)	5 (0.1)	–	146 (3.5)	8 (1.5)	7 (0.2)
<i>Phymorynchus</i> sp.	–	–	–	–	1 (0.0)	–	–
Polynoids	1 (0.1)	1 (0.0)	1 (0.0)	–	2 (0.0)	2 (0.4)	3 (0.1)
Anemones	168 (7.7)	512 (11.3)	2523 (74.9)	4 (0.3)	–	54 (9.8)	47 (1.5)
Cladorhizid sponge	–	5 (0.1)	–	–	–	–	–

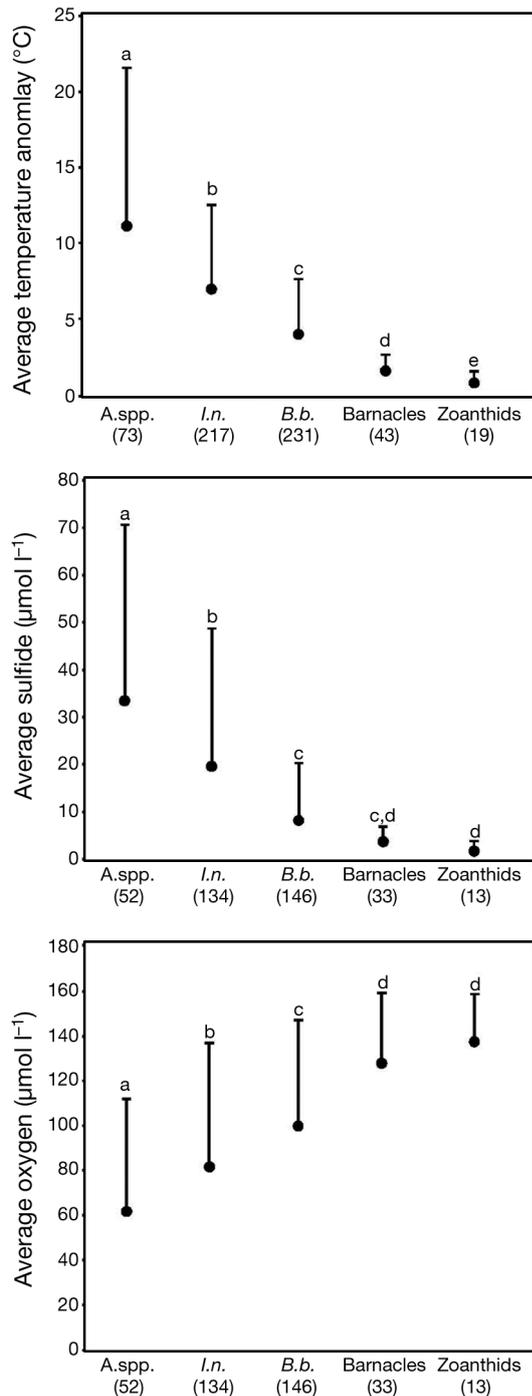


Fig. 3. Average temperature anomalies (°C above ambient temperature) and oxygen and sulfide concentrations across assessment sites experienced by each of the species in the aggregated faunal category. Significant differences (sequential Bonferroni correction, $p < 0.002$) are indicated by different letters over each standard deviation bar. The number of survey locations (n) taken among each species is listed below the species' name in parentheses. Data from mixed aggregations of *Bathymodiolus brevior* and *Ifremeria nautilei* were included in both species' categories for this analysis. A.spp.: *Alviniconcha* spp., I.n.: *Ifremeria nautilei*, B.b.: *Bathymodiolus brevior*

Only white *Alviniconcha* spp. were observed in TC1 and only dark *Alviniconcha* spp. in KM1. The 2 morphotypes of the snail were observed together in the other 3 assessment sites where the species occurred. Neither temperature nor concentrations of oxygen measured among white, dark, and mixed white and dark aggregations of *Alviniconcha* spp. were significantly different after a sequential Bonferroni correction. Sulfide was significantly higher among white aggregations compared to mixed ($W = 926.5$, $df = 1$, $p < 0.0044$), but was not significantly different from the dark morphotype.

Ifremeria nautilei was present in every assessment site and abundant in most, but very rare in TC2 (Table 3). Average temperature anomalies measured among aggregations of *I. nautilei* ranged from 0.4 to 29.4°C and the highest temperature measured was 32.5°C. Average sulfide concentrations ranged from undetectable to 129 μmol l⁻¹, and the highest sulfide concentration measured was 190 μmol l⁻¹. Average oxygen concentrations among *I. nautilei* ranged from undetectable to 179 μmol l⁻¹. Sulfide concentrations and temperatures measured among *I. nautilei* were significantly greater and oxygen concentrations were significantly lower than those measured among *Bathymodiolus brevior* (data from mixed aggregations of *I. nautilei* and *B. brevior* were included in the data sets for each respective species for this comparison), barnacles, and zoanithids (Fig. 3). When homogenous aggregations of *I. nautilei* and *B. brevior* were compared, highly significant differences in sulfide concentrations, temperatures, and oxygen concentrations were detected ($W = 8095$, $df = 1$, $p < 0.0001$; $W = 22027$, $df = 1$, $p < 0.0001$; and $W = 5679$, $df = 1$, $p < 0.003$, respectively).

White *Ifremeria nautilei* co-occurred with the dark *I. nautilei* morphotype in all but 2 assessment sites (TC2 and TM1) in which the morphotype was observed. Sulfide concentrations and temperatures were significantly higher ($W = 2695$, $df = 1$, $p < 0.0001$ and $W = 6076$, $df = 1$, and $p < 0.0001$, respectively) and oxygen concentrations were significantly lower among white *I. nautilei* compared to dark *I. nautilei* ($W = 962$, $df = 1$, $p < 0.0001$).

Bathymodiolus brevior was present at every site except TC2 (Table 3) and covered the greatest area in the northernmost assessment sites (20% at KM2 and 13% at KM1). Average temperature anomalies among *B. brevior* ranged from 0.1 to 28.6°C and the highest temperature measured was 32.0°C. Average sulfide concentrations measured among this species ranged from undetectable to 84 μmol l⁻¹, and the highest sulfide concentration measured was 132 μmol l⁻¹. Average oxygen concentrations ranged from undetectable to 180 μmol l⁻¹. Average temperatures measured

among *B. brevior* were significantly greater, and oxygen concentrations significantly lower than those measured among barnacles or zoanthids. Sulfide concentrations among the mussels were significantly greater than those among zoanthids, but they were not significantly different from those measured on barnacles (Fig. 3).

Mixed communities of *Ifremeria nautilei* and *Bathymodiolus brevior* were observed at 5 assessment sites and covered the greatest amount of area in the southernmost, andesite-hosted assessment sites (Table 3). Average temperature anomalies measured among these mixed aggregations ranged from 0.4 to 28.6°C, and the highest temperature measured was 32.0°C. Average sulfide concentrations ranged from undetectable to 84 $\mu\text{mol l}^{-1}$, and the highest concentration measured in a mixed aggregation was 131 $\mu\text{mol l}^{-1}$. Average oxygen concentrations ranged from undetectable to 179 $\mu\text{mol l}^{-1}$. Significantly lower sulfide concentrations and temperatures, and significantly higher oxygen concentrations were measured in mixed aggregations of *I. nautilei* and *B. brevior* compared to homogenous aggregations of *I. nautilei* ($W = 2259$, $df = 1$, $p < 0.0001$; $W = 3914$, $df = 1$, $p < 0.001$; $W = 6631$, $df = 1$, $p < 0.0001$ respectively). Sulfide and oxygen concentrations measured among mixed aggregations of *I. nautilei* and *B. brevior* were not significantly different from aggregations of *B. brevior*; however, temperatures measured among the mixed aggregations were significantly higher compared to homogenous aggregations of *B. brevior* ($W = 10411$, $df = 1$, $p < 0.0024$).

Barnacles were present in every assessment site and comprised 23% of the total aggregated faunal coverage in TC2 (3% out of 13%). Average temperature anomalies ranged from 0.2 to 5.1°C, and the highest temperature measured among barnacles was 9.5°C. Average sulfide concentrations measured on barnacles ranged from undetectable to 12 $\mu\text{mol l}^{-1}$, and the highest sulfide concentration measured was 17 $\mu\text{mol l}^{-1}$. Average oxygen concentrations ranged from 76 to 189 $\mu\text{mol l}^{-1}$. Temperatures measured among barnacles were significantly higher than those measured among zoanthids; however, oxygen and sulfide concentrations were not significantly different between the 2 faunal types (Fig. 3).

Zoanthids were observed only in 3 (of the 4) basalt-hosted sites (KM1, KM2, and TC1). Cover of this organism ranged from 2% (KM1) to 9% (TC1). Zoanthids were exposed to little or no hydrothermal flow; average temperature anomalies ranged from 0.0 to 2.6°C and average sulfide concentrations ranged from undetectable to 6 $\mu\text{mol l}^{-1}$. Temperature anomalies measured among zoanthids never exceeded 2.6°C and sulfide concentrations never exceeded 9 $\mu\text{mol l}^{-1}$.

Average oxygen concentrations ranged from 107 to 188 $\mu\text{mol l}^{-1}$.

Anemones were present in all assessment sites, except ABE1, and densities ranged from 0.3 to 74.9 m^{-2} (Table 3). Average temperature anomalies measured among anemone tentacles ranged from 0.2 to 4.4°C, and the highest temperature measured was 8.0°C. Average sulfide concentrations ranged from undetectable to 14 $\mu\text{mol l}^{-1}$. The highest sulfide concentration measured over anemones was 19 $\mu\text{mol l}^{-1}$. Average oxygen concentrations ranged from 78 to 162 $\mu\text{mol l}^{-1}$. Anemones were observed within 5 cm of symbiont-containing fauna more often than expected by the null hypothesis of random distribution at all sites where they were present, with the exception of KM1, and less often than expected directly on symbiont-containing fauna at all sites. Anemones were occasionally observed on shells of *Bathymodiolus brevior*.

Community composition across lava types

Relative cover of aggregated fauna was most similar among andesite-hosted communities (Bray-Curtis clustering; Fig. 4), but similarity was not significantly attributed to lava type (ANOSIM, Global R value =

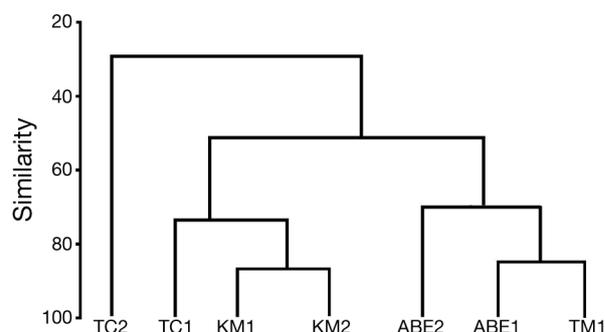


Fig. 4. Clustered (average linkage) Bray-Curtis similarity coefficients derived from relative cover of aggregated fauna within each assessment site

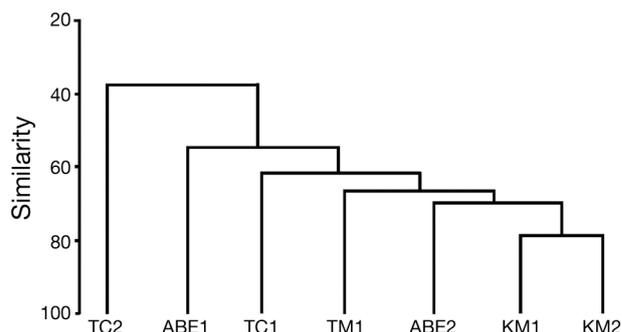


Fig. 5. Clustered (average linkage) Bray-Curtis similarity coefficients derived from densities of solitary fauna within each assessment site

0.352, $p > 0.1$). Similarity coefficients of solitary faunal densities did not cluster by lava type (Bray Curtis clustering; Fig. 5; ANOSIM, Global R value = 0.093, $p > 0.2$). Lava type did, however, explain a significant amount of the variation in relative cover of mixed aggregations of *Ifremeria nautilei* and *Bathymodiolus brevior*, as well as a significant amount of the variation in densities of the galatheid crabs *Munidopsis lauensis* and the fish *Thermobiotes mytilogeiton*, all of which were more abundant in andesite-hosted sites (Tables 4 & 5). Vent field was a significant factor in determining densities of *Paralomis hirtella* and *T. mytilogeiton* (Table 5).

Because of the unique abiotic and biotic attributes of TC2 (see Discussion for further description; Tables 2 & 3), analyses that investigated the effect of lava type on community composition were also performed without this site. After the removal of TC2, lava type was still not a significant factor in determining overall community similarity of either relative cover of aggregated fauna or solitary faunal density; however, the relative cover of *Ifremeria nautilei* and *Bathymodiolus brevior* and the density of *Chiridota hydrothermica* were significantly affected by lava type, while mixed aggregations of *I. nautilei* and *B. brevior* were not (all 4 faunal categories were absent or rare in TC2). Relative cover of *B. brevior* and densities of *C. hydrothermica* were significantly greater on basalt, while relative cover of *I. nautilei* was significantly greater on andesite.

Variograms of oxygen and particularly sulfide had a distinct spatial structure in andesite-hosted sites, but displayed no spatial structure in basalt-hosted sites (Fig. 6). Sulfide measurements on andesite were autocorrelated over a distance of 64 cm and oxygen mea-

Table 4. General linear model testing the influence of lava type and vent field (nested within lava type) on relative cover of aggregated fauna. * $p < 0.05$

Species	Factor	df	F statistic	p
<i>Alviniconcha</i> spp.	Lava type	1	0.03	0.870
	Vent field	2	1.03	0.456
<i>Ifremeria nautilei</i>	Lava type	1	5.65	0.098
	Vent field	2	0.51	0.645
Mixed <i>I. nautilei</i> & <i>Bathymodiolus brevior</i>	Lava type	1	13.76	0.034*
	Vent field	2	1.04	0.454
<i>Bathymodiolus brevior</i>	Lava type	1	1.12	0.367
	Vent field	2	3.75	0.153
Barnacles	Lava type	1	1.97	0.255
	Vent field	2	1.27	0.399
Zoanthids	Lava type	1	3.76	0.148
	Vent field	2	0.33	0.742

surements were autocorrelated over 53 cm. The nugget variance was low relative to the sill for both sulfide and oxygen in andesite-hosted sites (sulfide nugget variance = 0.1 and sill = 184.5; oxygen nugget variance = 273.0 and sill = 2026.0), indicating that most of the spatial variation of each factor was captured. There was no evident spatial structure in temperature variograms for either lava type (Fig. 6).

Distribution of solitary faunal species

Austinograea spp. were present in every assessment site and densities of these crabs were similar in all sites (Table 3). About 15% of the austinograeid crabs present could confidently be identified to the species level (Table 3). The austinograeids were non-randomly distributed across substratum types at 5 of the 7 assessment sites due to their frequent occurrence directly on or within 5 cm of symbiont-contain-

Table 5. General linear model testing the influence of lava type and vent field (nested within lava type) on densities of solitary faunal species. * $p < 0.05$

Species	Factor	df	F statistic	p
<i>Thermarces</i> sp.	Lava type	1	0.28	0.631
	Vent field	2	1.44	0.364
<i>Thermobiotes mytilogeiton</i>	Lava type	1	1447.53	0.000*
	Vent field	2	1206.27	0.000*
<i>Chiridota hydrothermica</i>	Lava type	1	4.89	0.114
	Vent field	2	0.58	0.610
<i>Austinograea</i> spp.	Lava type	1	2.48	0.213
	Vent field	2	6.23	0.086
<i>Munidopsis lauensis</i>	Lava type	1	16.86	0.026*
	Vent field	2	1.90	0.293
<i>Paralomis hirtella</i>	Lava type	1	3.88	0.144
	Vent field	2	16.81	0.023*
Shrimp	Lava type	1	0.01	0.916
	Vent field	2	0.37	0.719
<i>Vulcanolepas</i> sp.	Lava type	1	0.60	0.495
	Vent field	2	0.75	0.544
<i>Eosipho desbruyeresi</i>	Lava type	1	5.63	0.098
	Vent field	2	4.87	0.114
<i>Phymorynchus</i> sp.	Lava type	1	0.60	0.495
	Vent field	2	0.50	0.650
Polynoids	Lava type	1	2.68	0.200
	Vent field	2	0.27	0.778
Anemones	Lava type	1	0.75	0.450
	Vent field	2	0.09	0.913
Cladorhizid sponge	Lava type	1	0.60	0.495
	Vent field	2	0.75	0.544

*Significant at 95% confidence level

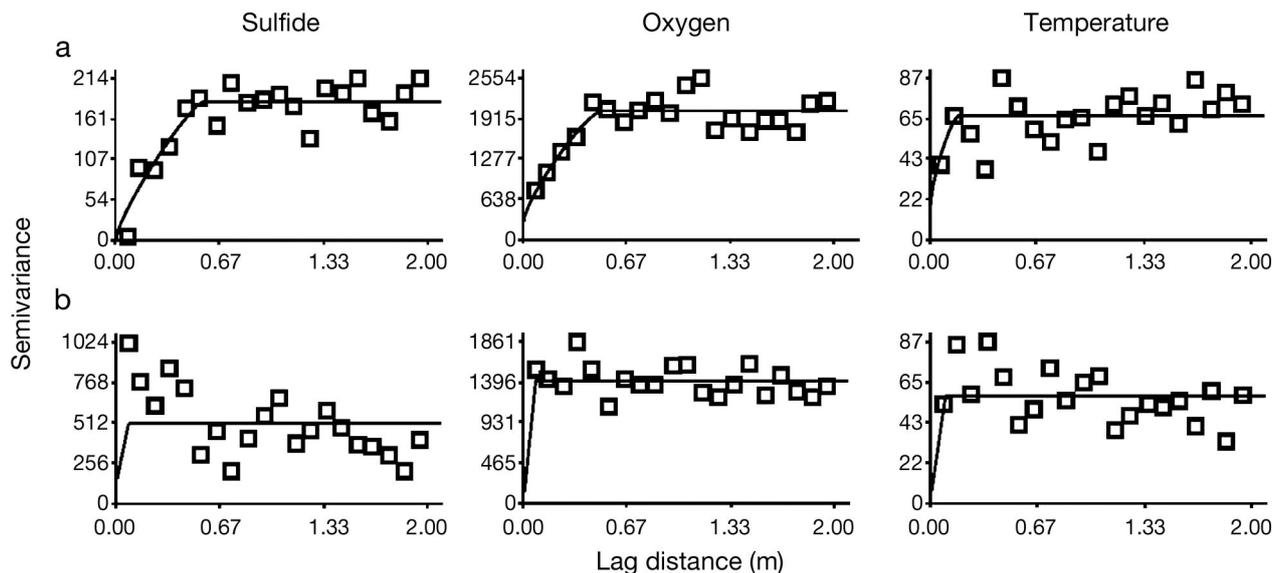


Fig. 6. Variograms of the chemical and thermal environments at (a) andesite-hosted sites and (b) basalt-hosted sites

ing fauna (Fig. 7). These crabs were rarely observed on barnacles and never on zoanthids (Fig. 8). Because there were no significant differences in the distribution patterns of the 2 species of austinograeid crab (Figs. 7 & 8), the species were combined for further analyses.

Of the 1293 shrimp observed in the mosaics, 19% could be reliably identified as *Alvinocaris komaii*. Shrimp were present in every assessment site and densities ranged from 0.1 to 10.4 m⁻². The 'other shrimp' group was non-randomly distributed in 3 of the 5 assessment sites with sufficient data for analysis and occurred on *Bathymodiolus brevior* significantly more than expected in 2 of the sites (Fig. 7). Similarly, *A. komaii* was non-randomly distributed in 3 of the 4 sites with sufficient data for analysis, and occurred on *B. brevior* more often than expected in all 4 sites (Fig. 7). Because *A. komaii* and 'other' shrimp had similar patterns of distribution at the 4 sites in which they could be differentiated (Fig. 7), they are hereafter considered as a single group.

The galatheid *Munidopsis lauensis* was observed in every assessment site, at significantly higher densities in andesite-hosted sites compared to basalt-hosted sites (GLM, $p < 0.03$; Table 5). At every site where sufficient individuals were present for χ^2 analyses ($n \geq 5$), the galatheid crabs were non-randomly distributed across substratum types (Fig. 7). *M. lauensis* were consistently observed on bare substrata and, if present, on zoanthids or barnacles. The galatheids were rarely present on symbiont-containing fauna (only 6% of the total observed population, Fig. 8) and never on *Alviniconcha* spp.

The snail *Eosipho desbruyeresi* was observed at every site except TC2 and was present in relatively high densities in ABE1 (3.5 m⁻²), the only site where a non-random distribution was detected (Fig. 7). The non-random distribution in ABE1 was primarily driven by the snail's preferential occurrence within 5 cm of symbiont-containing fauna (Fig. 7).

Most other solitary species occurred in relatively low numbers, which limited our ability to statistically examine their distributional patterns within a site. The stalked barnacle *Vulcanolepas* sp., the snail *Phymorhynchus* sp., and cladorhizid sponges were each only present in a single (different) site. The entire population of the fish *Thermobiotus mytilogeiton* and 50% of the population of the fish *Thermarces* sp. were observed in the ABE vent field. Holothurians (*Chiridota hydrothermica*) were observed in 3 of the 4 basalt-hosted assessment sites (KM1, KM2, and TC1). The larger anomuran crab, *Paralomis hirtella*, was present in 4 of the assessment sites (KM1, KM2, ABE1, and ABE2). Polynoids were present, but rare, in 6 of the 7 assessment sites and absent at TC2 (Table 3).

DISCUSSION

Distributions of symbiont-containing and attached fauna

The ELSC provides a natural laboratory to study animal distributions and the abiotic and biotic factors that synergistically define these distributions. Primary productivity is positively correlated with environmental

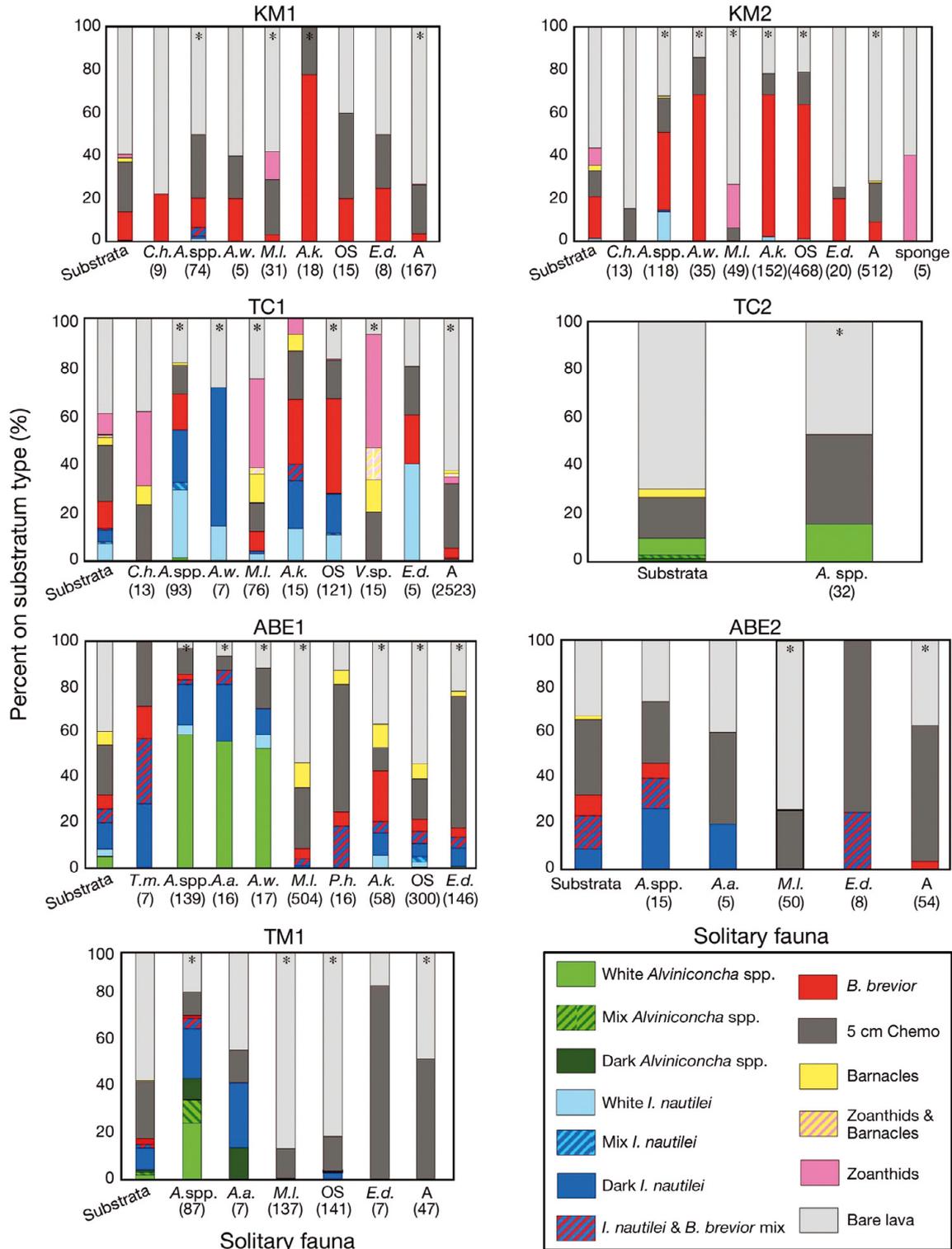


Fig. 7. Percent of the total population of each species of solitary fauna that occurred directly on a particular substratum type in each assessment site. Substratum types include aggregated fauna, bare substrata within 5 cm of symbiont-containing fauna ('5 cm Chemo'), and bare substrata more than 5 cm from symbiont-containing fauna ('bare lava'). Population size (n) is depicted in parentheses below each species of solitary fauna. χ^2 analyses tested the null hypothesis that solitary fauna were randomly distributed across all substrata types; * indicates that a distribution was significantly different from random (sequential Bonferroni correction, $p < 0.001$). *T.m.*: *Thermobiotes mytilogeiton*, *C.h.*: *Chiridota hydrothermica*, *A.spp.*: *Austinograea* spp., *A.a.*: *Austinograea alayseae*, *A.w.*: *Austinograea williamsi*, *M.l.*: *Munidopsis lauensis*, *P.h.*: *Paralomis hirtella*, *A.k.*: *Alvinocaris komaii*, *OS*: 'other' shrimp, *V. sp.*: *Vulcanolepas* sp., *E.d.*: *Eosipho desbruyeresi*, *P.*: polynoids, *A.*: anemones, sponge: cladorhizid sponge

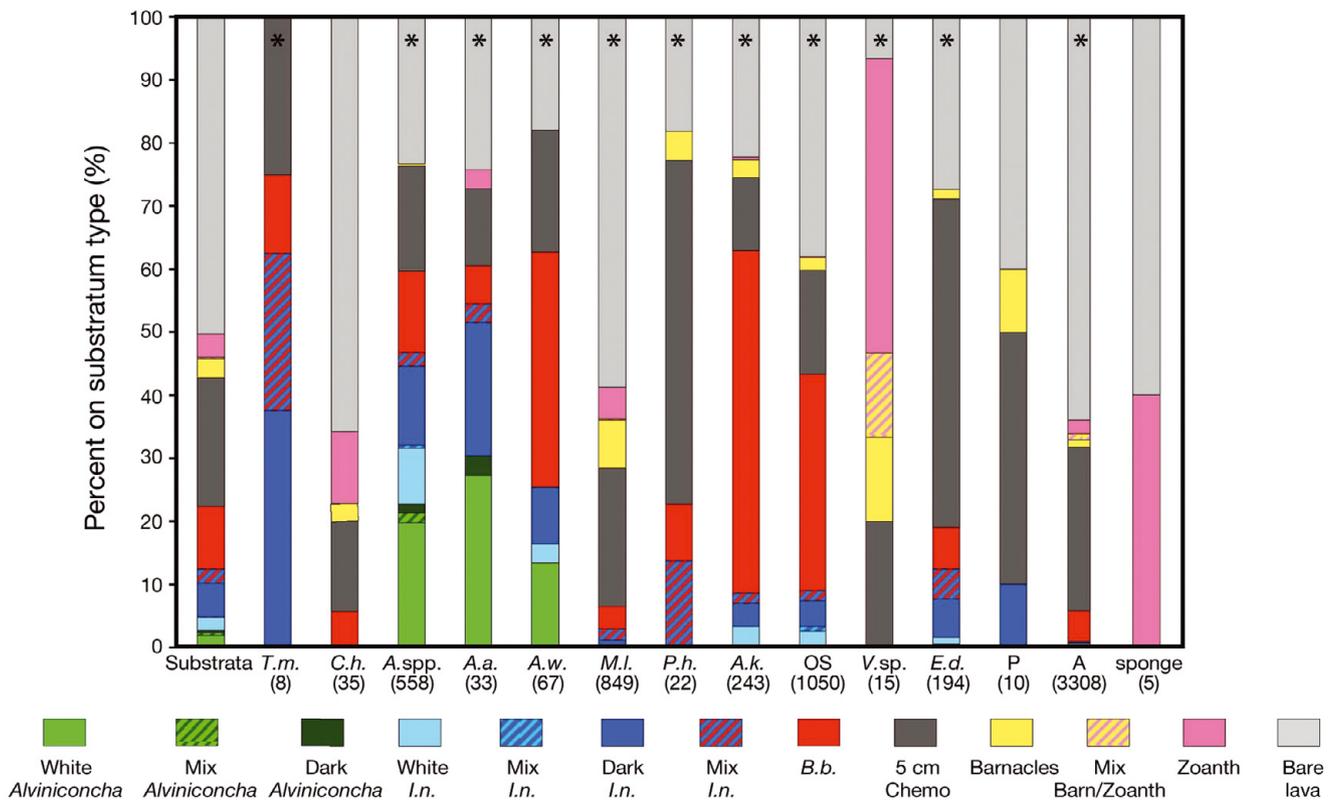


Fig. 8. Overall distribution of solitary faunal species (data from all assessment sites) across substratum types. Substratum types include aggregated fauna, bare substrata within 5 cm of symbiont-containing fauna ('5 cm Chemo'), and bare substrata more than 5 cm from symbiont-containing fauna ('bare lava'). Population size (n) is depicted in parentheses below each species of solitary fauna. χ^2 analyses tested the null hypothesis that solitary fauna were randomly distributed across all substratum types; * indicates that a distribution was significantly different from random (sequential Bonferroni correction, $p < 0.004$). See Fig. 7 legend for abbreviations of solitary faunal species

stressors at diffuse flow vent sites along the ELSC, a defining characteristic of all vent habitats, and the adults of all ELSC symbiont-containing species are mobile and can move if conditions become unsuitable in their immediate microhabitat. Therefore, the realized niches of most ELSC taxa will reflect a combination of the physiological requirements, preferences, and tolerances of the adults; current availability of local microhabitats; intraspecific interactions, and positive and/or negative interspecific interactions. Laboratory experiments (Henry et al. 2008) have provided insights to some of the abiotic factors defining the fundamental niches of the ELSC symbiont-containing fauna, and *in situ* studies and observations (Desbruyères et al. 1994, Desbruyères et al. 2006, Podowski et al. 2009) have laid the groundwork for understanding distributional patterns.

All vent metazoans are aerobic, and vent fluids are often hypoxic or anoxic. Oxygen availability is an important environmental variable limiting evolutionary invasion of these habitats, and many vent animals have special adaptations to facilitate oxygen uptake,

storage, and transport (Hourdez & Lallier 2007). However, the variation of diffuse hydrothermal flow at small spatial and temporal scales will normally allow mobile animals at least intermittent access to oxygen in most vent habitats occupied or visited by metazoans. On the other hand, sulfide can be toxic to aerobic respiration, and temperatures of vent fluid are often above the tolerance of any known metazoan (Childress & Fisher 1992). As a result, although average exposure to sulfide and temperature are likely to play a role in the distribution of most vent fauna, the upper limit of exposure to vent fluid is very likely set by an organism's tolerance for sulfide and/or high temperatures. One advantage of comparing multiple sites along the ELSC is that the sulfide content of the diffuse flow changes dramatically between vent fields (Table 2). This enables us to decouple, to a certain extent, the effects of sulfide and temperature, 2 variables that are strongly correlated in most vent habitats. In the case of the symbiont-containing taxa, a minimum requirement for sulfide to fuel chemoautotrophy will be an integral component of an organism's minimum requirement for

exposure to vent fluid. Within the limits set by these physiological requirements and tolerances, the realized niche of a particular symbiont-containing taxon may also be limited or expanded by interactions with other fauna (Jones et al. 1994, 1997, Micheli et al. 2002, Bruno et al. 2003, Mullineaux et al. 2003, Sancho et al. 2005).

Two color morphotypes (white and dark) of the 2 provannid snails were distinguishable in the images. At least 2 species of *Alviniconcha* occur on the ELSC; however, we did not detect significant differences in the chemistry or temperatures measured among homogenous aggregations of the 2 morphotypes of *Alviniconcha* spp., and we have no data to suggest that the color morphotypes distinguished in this study represent different species. Conversely, the sulfide concentrations and temperatures were significantly higher and oxygen concentrations lower among homogenous aggregations of the white morphotype of *Ifremeria nautilei* than the dark. Only a single species of *Ifremeria* has been described from the Western Pacific (Suzuki et al. 2006), there are no apparent differences in the morphology of the shells of the 2 color morphotypes, and only a single phylotype of *I. nautilei* has been detected in collections from the ELSC (B. Faure pers. comm.). We suggest the differences in color of *I. nautilei* in this study are due to either sulfide-oxidizing bacterial growth and the resultant precipitation of sulfur (Taylor & Wirsen 1997), or to hydrothermal staining, which is consistent with the general trends in chemistry associated with the color morphotypes. Presence of mixed aggregations of the 2 color morphotypes may reflect a combination of steep chemical and thermal gradients within areas of diffuse flow and mobility of the fauna.

Of the symbiont-containing fauna, *Alviniconcha* spp. occupied habitats with the greatest exposure to vent fluids. The highest temperature measured among *Alviniconcha* spp., 42.4°C, was higher than previously documented for this species (Desbruyères et al. 1994, Podowski et al. 2009). Temperatures of 44.5°C were measured on bare substratum adjacent to *Alviniconcha* spp. in ABE1, suggesting that the snail avoids temperatures near and above 45°C. Experiments with live animals corroborate this interpretation and demonstrated that *Alviniconcha* spp. could tolerate 45°C for a short period of time (30 min), but all specimens died when temperatures were elevated to 50°C (Henry et al. 2008). Also, *Alviniconcha* spp. ceases to induce heat shock protein synthesis at 44°C, demonstrating the snail's inability to deal with thermal stress at and above this temperature (Figueroa 2010). The highest level of sulfide we measured among *Alviniconcha* spp. in this study was 190 $\mu\text{mol l}^{-1}$, and a single measurement of 257 $\mu\text{mol l}^{-1}$ sulfide was measured among *Alvinicon-*

cha spp. in 2005 (Podowski et al. 2009). These sulfide concentrations are considerably below 400 $\mu\text{mol l}^{-1}$, the level correlated with peak sulfide and dissolved inorganic carbon (DIC) consumption in laboratory studies (Henry et al. 2008). It is unlikely that *Alviniconcha* spp. exposure to vent fluid is limited by sulfide tolerance on the ELSC; in the assessment site with the highest sulfide to temperature anomaly ratio measured in this study (TC2: 7.7 $\mu\text{mol l}^{-1} \text{ }^\circ\text{C}^{-1}$), the temperature of vent fluids with the laboratory-determined optimum sulfide concentration of 400 $\mu\text{mol l}^{-1}$ would be about 52°C, a temperature beyond the species' physiological tolerance. At all other sites the temperatures associated with this level of sulfide would be much higher. These data indicate that *Alviniconcha* spp. can occur in environments very near its thermal maxima without exposure to inhibitory concentrations of sulfide. We conclude that exposure of this snail to diffuse hydrothermal flow on the ELSC is limited by temperature tolerance, not sulfide toxicity.

Alviniconcha spp. has a relatively high metabolic rate and high autotrophic capacity, indicating substantial requirements for sulfide to support this very productive and likely fast-growing symbiosis (Henry et al. 2008). The minimum sulfide requirements of this snail are likely to play a significant role in its distribution; however, we were unable to define this snail's minimum requirements with data collected in this study.

Laboratory experiments performed with live animals maintained at in situ pressures demonstrated that *Ifremeria nautilei* has a similar temperature tolerance to *Alviniconcha* spp., but a much lower tolerance for sulfide (Henry et al. 2008). *I. nautilei* closes its operculum and halts sulfide and oxygen uptake at sulfide concentrations exceeding 100 $\mu\text{mol l}^{-1}$, suggesting that sulfide concentration, not temperature, may limit the distribution of *I. nautilei* in habitats suitable to *Alviniconcha* spp. This finding was not supported by our data. *I. nautilei* occupied habitats with the same range of sulfide concentrations as *Alviniconcha* spp.; however, temperatures above 33°C were never documented in association with *I. nautilei* (Fig. 9). It is important to note that sulfide levels above 100 $\mu\text{mol l}^{-1}$ were not common in the sites we surveyed. Furthermore, pH in diffuse flow among these sites can range from 6.1 to 7.0 (Hsu-Kim et al. 2008), and small differences in pH will affect the relative concentrations of HS^- and H_2S , an important consideration when *in situ* sulfide concentrations are similar to the experimentally determined sulfide limit as is the case for *I. nautilei*. Nonetheless, our data strongly suggest that temperature is more important than sulfide in determining the upper limits of exposure to vent fluid for *I. nautilei* on the ELSC.

Little is known about adaptations by *Alviniconcha* spp. and *Ifremeria nautilei*'s for the acquisition of oxy-

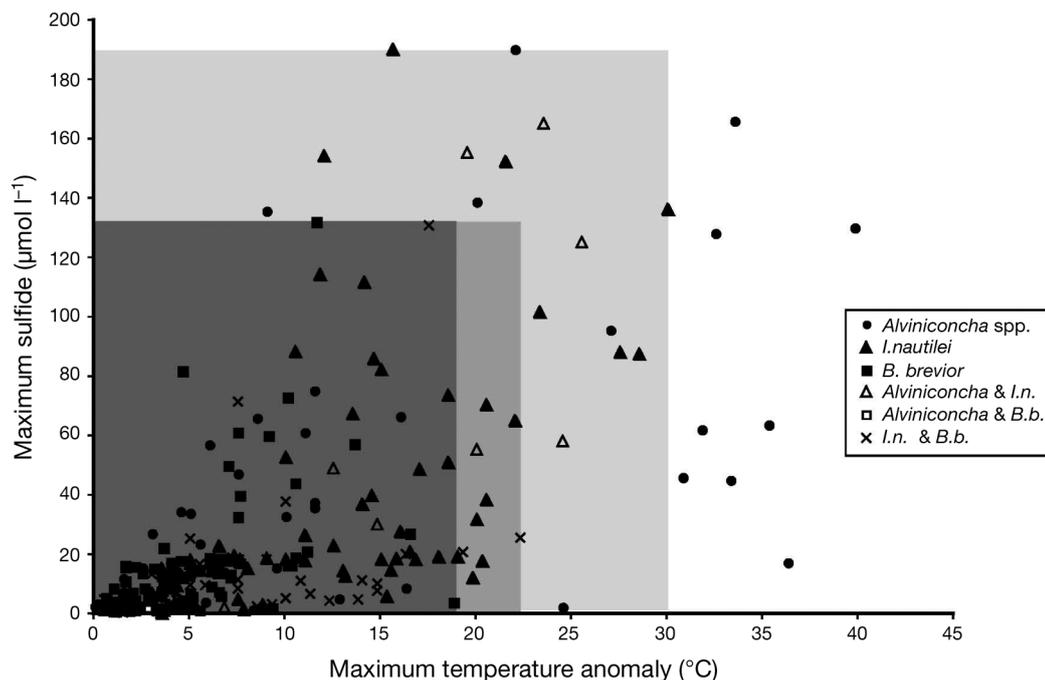


Fig. 9. Maximum sulfide and maximum temperature anomalies measured on symbiont-containing fauna from the 7 assessment sites. Dark grey highlights the extent of the range of *Bathymodiolus brevior*; intermediate grey highlights the extent of the range of mixed aggregations of *Ifremeria nautiliei* and *B. brevior*; light grey highlights the extent of the range of *I. nautiliei*; and the remaining space highlights the extent of the range of *Alviniconcha* spp.

gen from low environmental concentrations. The average oxygen concentrations found around *Alviniconcha* spp. were about 35% of ambient, and considerably lower concentrations were often documented. At these lower oxygen levels, differences in respiratory adaptations, including oxygen-binding pigments, may also exert a strong control on these snails' distributions.

There was considerable overlap in the range of abiotic habitats occupied by *Alviniconcha* spp. and *Ifremeria nautiliei* (Fig. 3), which suggests that positive and negative biological interactions will also be critical factors in defining these 2 species' distributional patterns. The average temperature measured around *Alviniconcha* spp. (13.6°C) is very close to the temperature associated with peak DIC uptake by *I. nautiliei* in laboratory experiments (13°C; Henry et al. 2008), suggesting *Alviniconcha* spp. may be able to exclude *I. nautiliei* from its preferred habitat. Furthermore, *in vitro* laboratory studies of the heat shock response in these 2 snails demonstrate that *Alviniconcha* spp. becomes thermally stressed around 34°C (induction of heat shock protein synthesis) and reaches its thermal maxima at 44°C (cessation of heat shock protein synthesis), while the onset of thermal stress for *I. nautiliei* occurs at about 26°C (Figueroa 2010). In this study, 14% of all temperatures measured on *Alviniconcha* spp. were within the snail's range of thermal stress (between 34 and 44°C), whereas only 3% of the tem-

peratures measured among *I. nautiliei* were indicative of thermal stress (above 26°C). *Alviniconcha* spp.'s ability to inhabit areas within a few degrees of its thermal maximum may give this species a competitive advantage over *I. nautiliei* when seeking optimal habitat.

Alternatively, laboratory data suggest *Ifremeria nautiliei* does not require as high a sulfide concentration as *Alviniconcha* spp. The high metabolic rate and autotrophic capacity of *Alviniconcha* spp. may enable this species to consume a significant portion of the sulfide in hydrothermal fluids, thus effectively extending the realized niche of *I. nautiliei* by creating suitable microhabitat conditions on the edges of *Alviniconcha* spp. aggregations. Clearly, understanding the biological interactions among these snails will be critical in defining their realized niches and will require *in situ* manipulative experiments.

Like the 2 snail species, the mussel *Bathymodiolus brevior* hosts sulfur-oxidizing symbionts in its gills (Dubilier et al. 1998), which are critical to the nutrition of bathymodiolin mussels (Childress & Fisher 1992). Based on studies of other vent bathymodiolins, we assume that this species may supplement its nutrition by filter feeding (Page et al. 1991), but also requires a minimal level of exposure to the reduced compounds in vent fluids to remain healthy (Smith 1985, Fisher et al. 1988). Laboratory studies demonstrated that *B. brevior* had a significantly lower thermal tolerance than

either snail (about 20°C), but that the mussel's tolerance for sulfide was intermediate between that of the 2 snails (Henry et al. 2008). The highest sulfide to temperature anomaly ratio measured in this study (TC2: 7.7 $\mu\text{mol l}^{-1} \text{ }^{\circ}\text{C}^{-1}$) would yield an average sulfide concentration of 150 $\mu\text{mol l}^{-1}$ at 20°C, a concentration well within the laboratory-determined sulfide tolerance of this species. Therefore, our data support the hypothesis proposed by Podowski et al. (2009) that temperature is more important than sulfide in determining the mussel's distribution (Fig. 9).

Although the chemical and thermal microhabitats occupied by *Ifremeria nautilei* and the mussel *Bathymodiolus brevior* are significantly different (Fig. 6), the 2 species often occur in mixed aggregations. Formation of these mixed aggregations appears to be determined first by temperature and then by lava type. Mixed aggregations experience significantly higher temperatures than homogenous aggregations of *B. brevior* and significantly lower temperatures compared to homogenous aggregations of *I. nautilei*. Mixed aggregations of the 2 species likely form when temperatures are near the upper extent of *B. brevior*'s range of tolerance. Only 3% of all temperatures measured among *B. brevior* were greater than 18°C, the approximate temperature at which heat shock protein synthesis is induced in the mussel (Figueroa 2010). Higher temperatures may cause thermal stress and diminish the mussel's competitive ability to exclude *I. nautilei*.

Mixed aggregations of *Ifremeria nautilei* and *Bathymodiolus brevior* were significantly more abundant in andesite-hosted than basalt-hosted sites (Table 4), and consideration of the differences in microhabitats associated with the 2 lava types yields insights into the reasons for this. Microhabitats within the apparent preference range of both *I. nautilei* and *B. brevior* were often documented on basalt, but these habitats were almost exclusively occupied by *B. brevior* (particularly apparent in KM2; Fig. 2). We hypothesize that *B. brevior* are more successful at excluding *I. nautilei* from mussel habitat on basalt for 3 interrelated reasons. First, pillow basalt provides a more solid substratum than andesite for attachment of byssal threads and stabilization of mussel beds (Hessler et al. 1988). Secondly, the friable texture, permeability (Hawkins 1995), and high vesicularity (Vallier et al. 1991) of andesite facilitates circulation of hydrothermal fluids across a larger area relative to the point source emissions through cracks in basalt-hosted sites (Fig. 6). As a result, adult mussels may not be able to monopolize the source of flow on andesite as they can on basalt (Johnson et al. 1988, 1994, Shank et al. 1998). Finally, securely attached mussel aggregations laterally diffuse hydrothermal fluids and consume sulfide (John-

son et al. 1994). The size of the mussel aggregation should be limited by the concentration of the sulfide at the edges of the aggregation and since the mussels have a low minimum requirement for sulfide, they can eventually monopolize the available vent flow to the exclusion of *I. nautilei*. As a result, the realized niche of *I. nautilei* is likely limited by biological interactions, by *Alviniconcha* spp. in the most active and by *B. brevior* in the least active areas of diffuse flow the snail could otherwise occupy. The distribution of *B. brevior* appears to be defined predominantly by abiotic factors; its upper extent of exposure to vent flow is limited by temperature, while its lower limits of exposure are regulated by a minimum requirement for reduced sulfur species in vent fluid.

Zoanthids and barnacles occurred in microhabitats with either undetectable or detectable but low exposure to vent fluids (Fig. 3). Zoanthids were only found in 3 of the basaltic sites (and none of the andesitic ones) and differences in abiotic environments (sulfide, oxygen, and temperature) were also tested using only data from the sites where these taxa co-occurred. The results were similar, although the differences in temperature were not significant ($p < 0.025$) after a sequential Bonferroni correction. Neither the zoanthids nor barnacles are known to harbor symbionts, and other known barnacles and zoanthids feed on particulates including plankton. Both can clearly tolerate minimal exposure to vent flow and neither is found in appreciable numbers more than a few meters away from a recognizable source of diffuse flow. We suggest that proximity to a source of diffuse flow and the associated primary and secondary production is limited by sulfide and/or temperature but necessary to sustain aggregations of either species. In the peripheral diffuse flow microhabitat they occupy, oxygen is close to ambient and is unlikely to exert a direct control on their distribution. Because the average temperature measured around barnacles was significantly higher than measured among zoanthids, and the barnacles were frequently observed attached to mussel shells (which are exposed to even more vent flow), we suggest that the barnacles can tolerate greater exposure to hydrothermal flow than the zoanthids and occupy some habitats that the zoanthids cannot.

The only other attached taxa of megafauna that were present in sufficient numbers for analysis of abiotic indicators of exposure to vent fluid were the anemones. As in the Kairei vent field on the Central Indian Ridge and other back-arc basins, anemones can be quite abundant in areas associated with diffuse flow on the ELSC (Van Dover et al. 2001, Van Dover 2002). There are at least 6 species of anemones near areas of diffuse flow along the ELSC (Zelnio et al. 2009), with *Actinostolidae* sp. and *Cyananthea hourdezi* being the

most abundant in this study. The average sulfide and temperatures measured on individual anemones was significantly above ambient ($3 \mu\text{mol l}^{-1}$ and $+1.4^\circ\text{C}$, respectively; $p < 0.0001$ for both); however, anemones in the diffuse flow areas were always exposed to oxygen, and maximum sulfide concentrations and temperatures never exceeded $19 \mu\text{mol l}^{-1}$ and 8.0°C , respectively. Anemones can therefore also tolerate low levels of exposure to hydrothermal flow in order to benefit from higher densities of potential prey associated with the enhanced local primary productivity. These abiotic tolerances are reflected in the anemones' distributional patterns (Fig. 7). It is also possible that some of these cnidarians species have chemoautotrophic symbionts, although to our knowledge there is no positive evidence to support this.

Differences between sites and lava types

The distribution of animals is a function of a variety of factors, including dispersal and recruitment processes, physiological requirements and tolerances, and both intra- and interspecific interactions (Connell 1961, Hutchinson 1965, Sarrazin & Juniper 1999, Bruno et al. 2003, Levesque et al. 2003). Dispersal and recruitment of the ELSC fauna have not been well studied; however, the relative proximity of the 4 vent fields, dispersal capabilities of other vent fauna (ie: Marsh et al. 2001, Won et al. 2003), the fact that most of the species are known from other back-arc basins in the western Pacific, and the occurrence of most species in all 4 vent fields suggest that dispersal capability is not preventing the majority of the fauna from reaching any of the assessment sites. It is therefore unlikely that the differences detected in faunal distributions among sites or between andesite and basalt along the ELSC reflects a dispersal barrier to larvae.

TC2 was the most hydrothermally active site containing 3 small (<1m) venting chimneys and diffuse fluids with the highest sulfide content of all assessment sites (with a sulfide to temperature anomaly ratio of $7.7 \mu\text{mol l}^{-1} \text{ }^\circ\text{C}^{-1}$). The faunal community at this site was also quite different from the other sites (Figs. 4, 5, & 9; supplement). We propose that the TC2 community represents an early successional stage of community development in recently activated hydrothermal flow on the ELSC. The dominance of a single, presumably fast-growing, symbiont-containing species (*Alviniconcha* spp.) in diffuse flow (Fig. 7), generally low species richness (Table 1), abundance of bythograeid crabs (Table 3), and presence of filter feeders (barnacles; Fig. 7) near sources of diffuse flow is analogous to the early stage of succession described by Shank et al. (1998) for the East Pacific Rise. Since the hypothesized

young age of this community may have a larger effect on the composition of the community than lava type, we made all comparisons of communities between lava types both including and excluding TC2.

A variety of parameters change with lava type along the ELSC. Along the length of the ELSC, depth varies from north to south from 2700 to 1875 m, and between the basaltic site Tow Cam and the andesitic site ABE, depth ranges from 2700 to 2100 m. Depth tolerance may account for the absence of some fauna (such as *Chiridota hydrothermica* in andesitic sites) on basalt and andesite. Chemistry also undoubtedly plays a very important role in defining local microhabitats and species' distributions; however, we hypothesized that the physical properties of the 2 lava types are also important factors in determining some species' distributions. Andesitic lavas are friable and permeable (Hawkins 1995), while basalt lavas in our study sites often occurred as smooth-surfaced, pillow structures (Ferrini et al. 2008). Furthermore, chemistry is spatially autocorrelated over larger distances (up to about 0.5 m) in andesite-hosted compared to basalt-hosted sites (Fig. 6), and this likely reflects differences in the lavas' physical properties. Despite these differences, lava type was not a significant factor explaining overall similarity of relative aggregated faunal cover or solitary faunal density among the assessment sites. The limited number of replicate assessment sites (4 on basalt and 3 on andesite) and the inherent variability among assessment sites (Table 2) likely reduced our ability to detect significant differences in this study. Nonetheless, lava type did explain a significant portion of the variability in some of the individual species' distributions among the assessment sites (Tables 4 & 5). The grouping of assessment site by lava type in Fig. 4 is in part a reflection of the high relative cover of mixed communities of *Bathymodiolus brevior* and *Ifremeria nautilei* and the absence of zoanthids in the andesite-hosted assessment sites. As discussed above, the physical properties of the basaltic lavas may facilitate *B. brevior's* exclusion of *I. nautilei* in habitats amenable to both species in the northern, basaltic sites. Although lava type did not significantly explain the variation in anemone density (Table 5), anemone densities were consistently greater in basalt-hosted sites compared to andesite-hosted sites, a trend that was even more evident when TC2 was excluded (Table 3; and see the supplement to compare patterns of anemone distribution in basalt and andesite-hosted sites). Compared to andesite, pillows of basalt provide a large smooth and hard surface for cnidarians, such as the anemones and zoanthids, to colonize. Basalt also allows animals to inhabit locations closer to diffuse flow (adjacent to high primary productivity), and still avoid most exposure to vent fluids, particularly sulfide (see TC1 digitized fauna in the supplement).

Distributions of other megafauna

Tissue stable isotope contents of all species of vent fauna analyzed to date indicate they obtain the bulk of their nutrition from local primary productivity (Fisher et al. 1994, Van Dover & Fry 1994, Van Dover 2000, Bergquist et al. 2007). Most species do not contain symbionts and either feed on free-living bacteria or consume these primary consumers. Free-living chemoautotrophic bacteria require exposure to reduced chemicals and therefore at least intermittent exposure to diffuse flow. Although not well quantified, the highest levels of standing stock biomass at vents are in areas of active diffuse flow, presumably reflecting the areas of highest primary production. In order to directly access this potentially abundant food source, mobile fauna must be able to tolerate some level of exposure to vent fluids.

Levels of exposure to vent fluid could not be measured directly for mobile fauna. However, considerable insight into the tolerances and preferences of some species can be inferred from their distributions relative to the symbiont-containing and other attached fauna whose habitat parameters were well documented and constrained. The bythograeid crab *Austinograea* spp. consistently demonstrated a preference for biological substrata in the most hydrothermally active areas within an assessment site (compare distribution across sites in Fig. 7). This observed distribution and laboratory-based physiological experiments suggest that *Austinograea* spp. has considerable tolerance for exposure to diffuse vent flow (Henry 2008), similar to the bythograeid vent crabs on the East Pacific Rise (Gorodezky & Childress 1994, Hourdez & Lallier 2007, Henry 2008). Although no potential predators of adult *Austinograea* spp. have been identified on the ELSC, it is worth noting that few metazoans are able to tolerate the conditions present in the areas of highest productivity at vents, so this is likely to be a predator-free zone for bythograeid crabs.

Shrimp were generally most abundant in areas of intermediate productivity, but rarely observed on *Alviniconcha* spp. Their distribution was quite similar to *Austinograea* spp. at the sites with few *Alviniconcha* spp. (Fig. 7), suggesting that this potential predator did not limit shrimp distribution. We suggest that the distribution of shrimp in a vent site is constrained by their preference for areas of highest productivity within their tolerance to vent flow, but that they cannot tolerate as high a level of exposure to vent fluid as *Alviniconcha* spp. and *Austinograea* spp. Although biological interactions may limit the shrimps' distribution in the peripheral areas of a vent site, we suggest that biological interactions do not limit their distribution at the upper end of their tolerance to vent fluid (cf. Van Dover 2002).

Galatheid crabs are a common deep-sea taxon and local species are often found in higher abundance near vents and seeps, which suggest that most species are vagrants and not vent specialists (Chevaldonné & Olu 1996, Martin & Haney 2005) and are likely have a low physiological tolerance to sulfide (Shank et al. 1998). Considering the relative robustness of their chelae, it is possible that *Austinograea* spp. may exclude *Munidopsis lauensis* from more productive areas. However, *M. lauensis* was rarely observed on any symbiont-containing fauna, even in the 3 sites where *Austinograea* spp. occurred on *Bathymodiolus brevior* significantly less than expected by the null model of random distribution (ABE1, ABE2, and TM1; Fig. 7). These data suggest that *M. lauensis* is also excluded from the areas of highest productivity in the vent environment by physiological constraints and not biological interactions. This is consistent with the higher densities of the galatheid in the southern andesitic sites (Table 2), where sulfide levels were generally lower.

CONCLUSIONS

Hydrothermal vent environments are extremely dynamic with large variations in environmental parameters on small spatial and temporal scales. The ELSC symbiont-containing megafauna are mobile throughout their lives, enabling these species to choose their preferred microhabitat and respond quickly to local changes in hydrothermal conditions. *Alviniconcha* spp. has the highest chemoautotrophic potential and metabolic rate (Henry et al. 2008), is the most active, and is found in the most robust areas of diffuse flow of the 3 dominant symbiont-containing fauna on the ELSC. This snail often experiences temperatures near its thermal maximum, and we suggest that its upper limit of exposure to vent fluid on the ELSC is limited by temperature, not chemistry or detectable biological interactions. *Alviniconcha* spp. is likely to have a moderately high requirement for sulfide, due to its high metabolic rate and a minimum requirement for exposure to vent fluid that is substantially higher than either *Ifremeria nautilei* or *Bathymodiolus brevior*.

On the other end of the diffuse flow exposure spectrum is the mussel *Bathymodiolus brevior*. The mussel's minimum requirement for reduced sulfur species will define its minimum requirement for exposure to dilute hydrothermal fluid. There is substantial overlap in what appear to be the optimum conditions for chemoautotrophy between *B. brevior* and *Ifremeria nautilei*. Thermal stress at about 20°C appears to limit *B. brevior*'s exposure to vent fluid above this temperature, but interactions between *I. nautilei* and *B. brevior* at lower temperatures and intermediate sulfide levels

will influence the distribution of *B. brevior* in some environments. Our data also indicate that *B. brevior* has an increased competitive advantage in basaltic sites where it can successfully exclude *I. nautiliei* to a greater degree than in andesitic sites.

Ifremeria nautiliei occupies an intermediate habitat, on average significantly different from that of the other symbiont-containing species with respect to sulfide, oxygen, and temperature. As noted above, at the low end of this snail's range, interactions with *Bathymodiolus brevior* will influence its realized niche. At the upper end of *I. nautiliei*'s range, where temperatures are amenable to *I. nautiliei* and sulfide levels approach the minimum required by *Alviniconcha* spp., biological interactions between the 2 snails will be an important determinant of their realized niches. Our data suggest that temperature, and perhaps oxygen, provide greater constraints on the distribution of *I. nautiliei* than sulfide on the ELSC; however, biological interactions appear to exert a strong influence over *I. nautiliei*'s distribution at both ends of its environmental range.

The only species of megafauna without intracellular chemoautotrophic symbionts that occupied the entire diffuse flow habitat colonized by symbiont-containing species were *Austinograea* spp. These crabs seek out the most active diffuse flow and highest presumed productivity in the local diffuse flow area. Shrimp often co-occur with these crabs, and their distribution does not appear to be limited by interactions with this crab. Shrimp, however, do not co-occur with *Alviniconcha* spp. and are likely unable to tolerate the high a level of exposure to vent fluid experienced by this snail or by *Austinograea* spp. Several groups, including barnacles, cnidarians, the crab *Paralomis hirtella*, and the snail *Eosipho desbruyeresi*, tolerate and even exhibit a preference for habitats with very low levels of exposure to hydrothermal fluid. As a result, these animals can more directly benefit from primary productivity associated with hydrothermal flow than other species, such as *Munidopsis lauensis*, that actively avoid exposure to hydrothermal fluid.

Lava type was a significant factor in determining distributional patterns of mixed communities of *Ifremeria nautiliei* and *Bathymodiolus brevior*, zoanthids, and *Munidopsis lauensis*. Consideration of what is known about the habit and biology of these groups suggests that the physical properties of the lavas are the most likely cause for the increased occurrence of mixed snail and mussel aggregations and absence of zoanthids on the more andesitic lavas; while the higher density of galatheid crabs in the andesitic sites is more likely explained by the generally lower sulfide levels associated with diffuse flow in the southern sites.

More precise determinations of the relative roles of dispersal, recruitment, biological interactions, temper-

ature, and chemistry in determining the distributions of the dominant megafaunal species on the ELSC will require additional study including manipulative experiments. Nonetheless, the data from this study, together with the results of laboratory experiments, allow us to constrain the effects of the aforementioned variables and formulate well-tuned hypotheses that serve as a foundation for ongoing studies of the western Pacific hydrothermal vent fauna.

Acknowledgements. This project was funded by National Science Foundation (NSF) grants OCE02-40985 and OCE07-32333 to CRF and NSF OCE-0240896 and OCE-0732439 to G.W.L. We thank the ROV 'Jason II' and RV 'Melville' crews for making this study possible and for their patience and expertise. We thank Kate Mullaugh and Tom Moore for their invaluable assistance with electrochemical data analysis, J. B. Moon for her assistance with variogram analyses, Erin Becker for many stimulating discussions with regard to the ecology of the ELSC, and Stephanie-Lessard Pilon, Dominique Cowart, Arunima Sen, Erin Becker, and Iliana Baums for comments and suggestions on earlier versions of the manuscript.

LITERATURE CITED

- Bergquist DC, Eckner JT, Urcuyo IA, Cordes EE, Hourdez S, Macko SA, Fisher CR (2007) Using stable isotopes and quantitative community characteristics to determine a local hydrothermal vent food web. *Mar Ecol Prog Ser* 330:49–65
- Bouchet P, Warén A (1991) *Ifremeria nautiliei*, a new gastropod from hydrothermal vents, probably associated with symbiotic bacteria. *C R Acad Sci (Paris) Ser III* 312: 495–501
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18: 119–125
- Chevaldonné P, Olu K (1996) Occurrence of anomuran crabs (crustacea: Decapoda) in hydrothermal vent and cold-seep communities: a review. *Proc Biol Soc Wash* 109:286–298
- Childress JJ, Fisher CR (1992) The biology of hydrothermal vent animals: physiology, biochemistry and autotrophic symbioses. *Oceanogr Mar Biol Annu Rev* 30:337–441
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723
- Corstanje R, Grunwald S, Reddy KR, Osborne TZ, Newman S (2006) Assessment of the spatial distribution of soil properties in a northern everglades marsh. *J Environ Qual* 35: 938–949
- Desbruyères D, Alayse-Danet AM, Ohta S and others (1994) Deep-sea hydrothermal communities in southwestern Pacific back-arc basins (the North Fiji and Lau Basins): composition, microdistribution and food web. *Mar Geol* 116:227–242
- Desbruyères D, Almeida A, Biscoito M, Comtet T and others (2000) A review of the distribution of hydrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls. *Hydrobiologia* 440: 201–216
- Desbruyères D, Biscoito M, Caprais JC, Colaco A and others (2001) Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic ridge near the Azores plateau. *Deep-Sea Res I* 48:1325–1346

- Desbruyères D, Hashimoto J, Fabri MC (2006) Composition and biogeography of hydrothermal vent communities in western Pacific back-arc basins. In: Christie DM, Fisher CR, Lee SM, Givens S (eds) Back-arc spreading systems; geological, biological, chemical, and physical interactions, Geophysical Monograph Series Vol 166. American Geophysical Union, Washington, DC, p 215-234
- Dubilier N, Windoffer R, Giere O (1998) Ultrastructure and stable carbon isotope composition of the hydrothermal vent mussels *Bathymodiolus brevior* and *B. sp. affinis brevior* from the North Fiji Basin, western Pacific. Mar Ecol Prog Ser 165:187–193
- Endow K, Ohta S (1989) The symbiotic relationship between bacteria and a mesogastropod snail, *Alviniconcha hessleri*, collected from hydrothermal vents of the Mariana back-arc basin. Bull Jap Soc Microb Ecol 3:73–82
- Ferrini VL, Tivey MK, Carbotte SM, Martinez F, Roman C (2008) Variable morphologic expression of volcanic, tectonic, and hydrothermal processes at six hydrothermal vent fields in the Lau back-arc basin. Geochem Geophys Geosyst 9:Q07022 doi: 10.1029/2008GC002047
- Figueroa D (2010) The heat shock response and thermal biology of selected hydrothermal vent organisms. PhD thesis, University of California, Santa Barbara, CA
- Fisher CR, Childress JJ, Arp AJ, Brooks JM and others (1988) Microhabitat variation in the hydrothermal vent mussel, *Bathymodiolus thermophilus*, at the Rose Garden vent on the Galapagos Rift. Deep-Sea Res 35:1769–1791
- Fisher CR, Childress JJ, Macko SA, Brooks JM (1994) Nutritional interactions in Galapagos Rift hydrothermal vent communities: inferences from stable carbon and nitrogen isotope analyses. Mar Ecol Prog Ser 103:45–55
- Gorodezky LA, Childress JJ (1994) Effects of sulfide exposure history and hemolymph thiosulfate on oxygen-consumption rates and regulation in the hydrothermal vent crab *Bythograea Thermydron*. Mar Biol 120:123–131
- Govenar BW, Bergquist DC, Urcuyo IA, Eckner JT, Fisher CR (2002) Three *Ridgeia piscesae* assemblages from a single Juan de Fuca Ridge sulphide edifice: structurally different and functionally similar. Cah Biol Mar 43:247–252
- Hawkins JWJ (1995) The geology of the Lau Basin. In: Taylor B (ed) Backarc basins: tectonics and magmatism. Plenum Press, New York, NY, p 63–138
- Henry M (2008) Sulfide oxidation in chemoautotrophic and heterotrophic invertebrates from hydrothermal vent and estuarine habitats. PhD thesis, University of California, Santa Barbara, NY
- Henry MS, Childress JJ, Figueroa D (2008) Metabolic rates and thermal tolerances of chemoautotrophic symbioses from Lau Basin hydrothermal vents and their implications for species distributions. Deep-Sea Res 55:679–695
- Hessler RR, Smithey WM, Keller CH (1985) Spatial and temporal variation of giant clams, tubeworms and mussels at deep-sea hydrothermal vents. Bull Biol Soc Wash 6: 411–428
- Hessler RR, Smithey WM, Boudrias MA, Keller CH, Lutz RA, Childress JJ (1988) Temporal change in megafauna at the Rose Garden hydrothermal vent (Galapagos Rift; eastern tropical Pacific). Deep-Sea Res 35:1681–1709
- Hourdez S, Lallier FH (2007) Adaptations to hypoxia in hydrothermal-vent and cold-seep invertebrates. Rev Environ Sci Biotechnol 6:143–159
- Hsu-Kim H, Mullaugh KM, Tsang JJ, Yucel M, Luther GWI (2008) Formation of Zn- and Fe- sulfides near hydrothermal vents at the Eastern Lau Spreading Center: implications for sulfide bioavailability to chemoautotrophs. Geochem Trans 9:6
- Hutchinson G (1965) The niche: an abstractly inhabited hypervolume. In: The ecological theatre and the evolutionary play. Yale University Press, New Haven, CT, p 26–78
- Johnson RA, Wichern DW (2007) Multivariate linear regression models. In: Applied multivariate statistical analysis. Pearson Education, Upper Saddle River, NJ, p 360–417
- Johnson KS, Childress JJ, Beehler CL (1988) Short-term temperature variability in the rose garden hydrothermal vent field: an unstable deep-sea environment. Deep-Sea Res 35:1711–1721
- Johnson KS, Childress JJ, Beehler CL, Sakamoto CM (1994) Biogeochemistry of hydrothermal vent mussel communities: the deep-sea analogue to the intertidal zone. Deep-Sea Res 41:993–1011
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386
- Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957
- Levesque C, Juniper SK, Marcus J (2003) Food resource partitioning and competition among alvinellid polychaetes of Juan de Fuca Ridge hydrothermal vents. Mar Ecol Prog Ser 246:173–182
- Luther GWI, Rozan TF, Taillefert M, Nuzzio DB and others (2001) Chemical speciation drives hydrothermal vent ecology. Nature 410:813–816
- Marsh AG, Mullineaux LS, Young CM, Manahan DT (2001) Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. Nature 411:77–80
- Martin JW, Haney TA (2005) Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2005. Zool J Linn Soc 145:445–522
- Martinez F, Taylor B (2002) Mantle wedge control on back-arc crustal accretion. Nature 416:417–420
- Martinez F, Taylor B, Baker ET, Resing JA, Walker SL (2006) Opposing trends in crustal thickness and spreading rate along the back-arc Eastern Lau Spreading Center: implications for controls on ridge morphology, faulting, and hydrothermal activity. Earth Planet Sci Lett 245:655–672
- Micheli F, Peterson CH, Mullineaux LS, Fisher CR and others (2002) Predation structures communities at deep-sea hydrothermal vents. Ecol Monogr 72:365–382
- Mullineaux LS, Peterson CH, Micheli F, Wills SW (2003) Successional mechanism varies along a gradient in hydrothermal fluid flux at deep-sea vents. Ecol Monogr 73: 523–542
- Nuzzio DB, Taillefert M, Cary SC, Reysenbach AL, Luther GWI (2002) In situ voltammetry at hydrothermal vents. In: Taillefert M, Rozan T (eds) Environmental electrochemistry: analyses of trace element biogeochemistry, Vol 811. American Chemical Society, Washington, DC, p 40–53
- Okutani T, Ohta S (1988) A new gastropod mollusk associated with hydrothermal vents in the Mariana Back-Arc Basin, Western Pacific. Venus 47:1–9
- Page HM, Fiala-Medioni A, Fisher CR, Childress JJ (1991) Experimental evidence for filter-feeding by the hydrothermal vent mussel, *Bathymodiolus thermophilus*. Deep-Sea Res 38:1455–1461
- Parson LM, Pearce JA, Murton BJ, Hodkinson RA, Party RCDS (1990) Role of ridge jumps and ridge propagation in the tectonic evolution of the Lau back-arc basin, southwest Pacific. Geology 18:470–473
- Pizarro O, Singh H (2003) Towards large area mosaicing for underwater scientific applications. IEEE J Ocean Eng Special Issue on Underwater Image and Video Processing 28:651–672

- Podowski EL, Moore TS, Zelnio KA, Luther GWI, Fisher CR (2009) Distribution of diffuse flow megafauna in two sites on the Eastern Lau Spreading Center, Tonga. *Deep-Sea Res I* 56:2041–2056
- Press F, Siever R (1974) *Earth*. W. H. Freeman, New York
- Ryan WBF, Carbotte SM, Coplan JO, O'Hara S and others (2009) Global multi-resolution topography synthesis. *Geochem Geophys Geosyst* 10, Q03014 doi:10.1029/2008GC002332
- Sancho G, Fisher CR, Mills S, Micheli F and others (2005) Selective predation by the zoarcid fish *Thermarces cerberus* at hydrothermal vents. *Deep-Sea Res I* 52:837–844
- Sarrazin J, Juniper SK (1999) Biological characteristics of a hydrothermal edifice mosaic community. *Mar Ecol Prog Ser* 185:1–19
- Sarrazin J, Juniper SK, Massoth G, Legendre P (1999) Physical and chemical factors influencing species distributions on hydrothermal sulfide edifices of the Juan de Fuca Ridge, northeast Pacific. *Mar Ecol Prog Ser* 190:89–112
- Seewald J, McCollom T, Proskurowski G, Reeves G and others (2005) Aqueous volatiles in Lau Basin hydrothermal fluids. ESO Transactions of AGU 86: Fall Meeting Supplement, Abstract T31A-0478
- Shank TM, Fornari DJ, Von Damm KL, Lilley MD, Haymon RM, Lutz RA (1998) Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9° 50' N, East Pacific Rise). *Deep-Sea Res II* 45:465–515
- Smith KLJ (1985) Deep-sea hydrothermal vent mussels: nutritional state and distribution at the Galapagos Rift. *Ecology* 66:1067–1080
- Suzuki Y, Sasaki T, Suzuki M, Nogi Y and others (2005a) Novel chemoautotrophic endosymbiosis between a member of the Epsilonproteobacteria and the hydrothermal-vent gastropod *Alviniconcha* aff. *hessleri* (Gastropoda: Provannidae) from the Indian Ocean. *Appl Environ Microbiol* 71:5440–5450
- Suzuki Y, Sasaki T, Suzuki M, Tsuchida S, Neelson KH, Horikoshi K (2005b) Molecular phylogenetic and isotopic evidence of two lineages of chemoautotrophic endosymbionts distinct at the subdivision level harbored in one host-animal type: the genus *Alviniconcha* (Gastropoda: Provannidae). *FEMS Microbiol Lett* 249:105–112
- Suzuki Y, Kojima S, Watanabe H, Suzuki M and others (2006) Single host and symbiont lineages of hydrothermal vent gastropods *Ifremeria nautilei* (Provannidae): biogeography and evolution. *Mar Ecol Prog Ser* 315:167–175
- Taylor B, Martinez F (2003) Back-arc basin basalt systematics. *Earth Planet Sci Lett* 210:481–497
- Taylor CD, Wirsén CO (1997) Microbiology and ecology of filamentous sulfur formation. *Science* 277:1483–1485
- Taylor B, Zellmer K, Martinez F, Gooday A (1996) Sea-floor spreading in the Lau back-arc basin. *Earth Planet Sci Lett* 144:35–40
- Tunnicliffe V, Fowler CMR (1996) Influence of sea-floor spreading on the global hydrothermal vent fauna. *Nature* 379:531–533
- Urakawa H, Dubilier N, Fujiwara Y, Cunningham DE, Kojima S, Stahl DA (2005) Hydrothermal vent gastropods from the same family (Provannidae) harbour ϵ - and γ -proteobacterial endosymbionts. *Environ Microbiol* 7:750–754
- Vallier TL, Jenner GA, Frey FA, Gill JB and others (1991) Subalkaline andesite from Valu Fa ridge, a back-arc spreading center in southern Lau Basin: petrogenesis, comparative chemistry, and tectonic implications. *Chem Geol* 91:227–256
- Van Dover CL (2000) The ecology of deep-sea hydrothermal vents. Princeton University Press, Princeton, NJ
- Van Dover CL (2002) Trophic relationships among invertebrates at the Kairei hydrothermal vent field (Central Indian Ridge). *Mar Biol* 141:761–772
- Van Dover CL (2003) Variation in community structure within hydrothermal vent mussel beds of the East Pacific Rise. *Mar Ecol Prog Ser* 253:55–66
- Van Dover CL, Fry B (1994) Microorganisms as food resources at deep-sea hydrothermal vents. *Limnol Oceanogr* 39: 51–57
- Van Dover CL, Humphris SE, Fornari DJ, Cavanaugh CM and others (2001) Biogeography and ecological setting of the Indian Ocean hydrothermal vents. *Science* 294: 818–823
- Van Dover CL, German CR, Speer KG, Parson LM, Vrijenhoek RC (2002) Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295:1253–1257
- von Cosel R, Metivier B, Hashimoto J (1994) Three new species of Bathymodiulus (Bivalvia: Mytilidae) from hydrothermal vents in the Lau Basin and the North Fiji Basin, Western Pacific, and the Snake Pit area, Mid-Atlantic Ridge. *Veliger* 37: 374–392
- Wackernagel H (1995) Multivariate geostatistics: an introduction with applications. Springer, Berlin
- Windoffer R, Giere O (1997) Symbiosis of the hydrothermal vent gastropod *Ifremeria nautilei* (Provannidae) with endobacteria: structural analyses and ecological considerations. *Biol Bull* 193:381–392
- Won Y, Young CR, Lutz RA, Vrijenhoek RC (2003) Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: *Bathymodiulus*) from eastern Pacific hydrothermal vents. *Mol Ecol* 12:169–184
- Zelnio KA, Rodriguez E, Daly M (2009) Hexacorals (Anthozoa: Actiniaria, Zoanthidea) from hydrothermal vents in the south-western Pacific. *Mar Biol Res* 5:547–571

Editorial responsibility: Paul Snelgrove,
St. John's, Newfoundland, Canada

Submitted: March 30, 2010; Accepted: August 27, 2010
Proofs received from author(s): November 11, 2010