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Community succession in hydrothermal vent habitats of the Eastern Lau Spreading Center and Valu Fa Ridge, Tonga

Arunima Sen,^{1,a,*} Elizabeth L. Podowski,^{1,b} Erin L. Becker,¹ Erica A. Shearer,¹ Amy Gartman,² Mustafa Yücel,^{2,c} Stéphane Hourdez,³ George W. Luther, III,² and Charles R. Fisher¹

¹Pennsylvania State University, Department of Biology, University Park, Pennsylvania

²School of Marine Science and Policy, University of Delaware, Delaware

³Station Biologique de Roscoff, Centre National de la Recherche Scientifique-Université Pierre et Marie Curie, Génétique des Adaptations au Milieu Extrême, Roscoff, France

Abstract

Patterns of succession in Lau Basin hydrothermal vent communities determined with high-resolution imagery and in situ physico-chemical data collected over 4 yr and analyzed within a Geographic Information System show that *Alviniconcha* snails are a pioneering group, the snail *Ifremeria nautilei* is a mid-successional species, and the heat-intolerant mussel *Bathymodiolus brevior* dominates when venting declines. The associated fauna also changes as communities progress through the successional stages, and eventually non-vent-endemic deep-sea species appear when venting has mostly subsided. This is a unique example of primary succession in which the primary producers form symbiotic associations with mobile animals, resulting in successional patterns not observed in other systems. *I. nautilei* dominates newly formed substrates or venting sources where both *I. nautilei* and *Alviniconcha* spp. are already established (e.g., by migration), while *Alviniconcha* spp. seem to be better at colonizing newly active vents (e.g., by settlement) that are remote from colonized vents. Thus, on the scale of a 5–39 m² diffuse flow area or a single edifice, the mid-successional species dominates new substrates instead of the pioneering group. These communities are remarkably stable over long time periods relative to other hydrothermal vent regions. In addition to the sequential replacements of species as sites age and overall conditions change, Lau vent animals track changes in vent fluids and relocate themselves when local hydrothermal plumbing changes over small spatial scales.

Succession is a central but contentious concept of ecological theory that has evolved through many differing viewpoints (Gleason 1927; Clements 1936; also *see* review by McCook [1994]). Even the accepted definition of succession varies, although most consider it to be a directional change in a community over time after a disturbance, often leading to sequential replacements of species (Margalef 1963; Odum 1969; McCook 1994). Despite the fact that succession is a hotly debated ecological concept, most models still retain a fairly narrow approach. Terrestrial systems and plants are the main focus of successional theory, and in fact, the word vegetation is commonly used in definitions of succession or stages of succession such as climax communities (Clements 1936; McCook 1994).

Animal succession was recognized as far back as Smith (1928). Connell and Slatyer (1977) included animals in their

models, although changes in the animal community were only considered as a reflection of the changes in the plant community or sessile organisms (Odum 1950; Väisänen and Järvinen 1977; Antoniadou et al. 2010). Recent studies have shown that animals can affect the succession of vegetation in several ways, such as dispersal of propagules, herbivory, or decomposition in both terrestrial (Majer 1989; Brown and Gange 1992; Kaufmann 2001) and aquatic systems (Dudley and D'Antonio 1991; McCormick and Stevenson 1991; Hixon and Brostoff 1996). Although most models of succession consider the role of animals to be minor (*see* review by Edwards and Gillman 1987), studies on systems where animals comprise a large portion of the biomass, such as in intertidal communities (Sousa 1984; Farrell 1989, 1991), subtidal communities (Breitburg 1985), marine benthic communities (Gallagher et al. 1983; Nilsson and Rosenberg 2000; Glover et al. 2010), stream communities (Resh et al. 1988; Matthaei and Townsend 2000), and even deep-sea systems such as cold seeps (Cordes et al. 2005; Lessard-Pilon et al. 2010) and hydrothermal vents (Sarrazin et al. 1997; Govenar et al. 2004; Cuvelier et al. 2009), are challenging this dogma. Glacial ecologists have even suggested that insect colonization can precede and catalyze vegetation colonization (Hodkinson et al. 2002; Coulson et al. 2003; Hågvar 2010).

Here we examine succession in hydrothermal vent communities of the Western Pacific, where animals with chemoautotrophic symbionts dominate the autotrophic biomass. The communities examined in this study are unique, because the dominant fauna harbor chemoautotrophic

* Corresponding author: Arunima.Sen@ifremer.fr

Present addresses:

^aInstitut français de recherche pour l'exploitation de la mer (IFREMER), Laboratoire Environnement Profond, Plouzané, France

^bNational Oceanic and Atmospheric Administration Coastal Management, New York Department of State, Albany, New York

^cGEOMAR Helmholtz Centre for Ocean Research Kiel, Department of Marine Biogeochemistry, Marine Geosystems Research Unit, Kiel, Germany

bacterial symbionts that form the base of the food chain and are functionally primary producers. Additionally, they are mobile and provide habitat for other smaller species of vent-dwelling fauna. The idea of species turnover (replacement of 'early successional' species with 'later successional' species over time) is integral to successional theory and easily observed where environmental conditions change and the species are incapable of moving. Typically the result is a die-off of certain species and the recruitment and growth of others, resulting in species turnover that is, in many cases, sequential and predictable. Our study examines the role of mobility in the successional process and, importantly, where succession of these mobile animals is not a response to changing sessile assemblages or vegetation. In addition to their unique ecology, Western Pacific vents are of interest because these vents are likely to be subject to mining for their polymetallic sulfide deposits in the near future (Van Dover 2011). Thus, understanding natural succession and change in these communities is a critical step toward formulating environmental assessment policies and interpreting post-mining studies.

Hydrothermal vent communities are found in all the world's oceans where new ocean floor is being created, such as at mid-ocean ridges and back-arc basins (Fisher et al. 2007). The discovery of vents expanded the general perception of where life can thrive, because the primary source of energy in vent systems is chemical instead of solar (Childress and Fisher 1992; Van Dover 2000). Vent waters are loaded with reduced compounds that can be utilized by chemoautotrophic bacteria as an energy source to fuel carbon fixation. At vents, these chemoautotrophic bacteria can either be free-living or they can form symbiotic relationships with metazoan species, resulting in huge standing crops of biomass that are in stark contrast with most of the deep sea (Grassle 1985; Van Dover 2000). Relying on the energy-rich vent effluent for food, however, comes with considerable cost. Hydrothermal effluent is very hot; end-member fluids reach 400°C. Diffuse venting results in lower temperatures, in the tens of degrees as opposed to in the hundreds of degrees (Lilley et al. 1983; Johnson et al. 1986), but even these fluids can reach temperatures beyond the limits of metazoan life. Furthermore, vent fluid is anoxic and high in hydrogen sulfide, which is one of the most abundant and commonly used chemoautotrophic energy sources (Jannasch and Mottl 1985) but is also toxic to metazoans even in micromolar concentrations (Beauchamp et al. 1984; Truong et al. 2006). Vents are also extremely dynamic and are characterized by very steep gradients in chemistry and temperature over very short distances and timescales. Therefore, animals that live in such environments must deal with heat, low levels of oxygen, sulfide toxicity, and extreme temporal and spatial fluctuations of all these conditions (Childress and Fisher 1992; Van Dover 2000).

This study was conducted in the hydrothermal vents of the Eastern Lau Spreading Center (ELSC) and Valu Fa Ridge (VFR), a back-arc basin located between the island countries of Fiji and the Kingdom of Tonga. The vent communities here are dominated by three groups of

mollusks that harbor sulfide-oxidizing bacteria in their gills (Desbruyères et al. 1994; Podowski et al. 2009, 2010), referred to as symbiont-containing mollusks or the symbiont-containing fauna throughout this manuscript. These mollusks are the provannid gastropods *Alviniconcha* spp. and *Ifremeria nautilei* and the mytilid bivalve *Bathymodiolus brevior*. Three different species of *Alviniconcha* have recently been identified on the ELSC, which have symbiotic relationships with at least three taxa of symbionts resulting in at least four different holobiont combinations (Beinart et al. 2012). However, the *Alviniconcha* spp. are morphologically cryptic, and for this image-based study we treat them collectively.

Prior work conducted in the Lau Basin revealed that the symbiont-containing mollusks inhabit distinct thermal and chemical niches (Podowski et al. 2009, 2010). *Alviniconcha* spp. are associated with the highest temperatures (2.4°C to 42.4°C) and levels of sulfide (undetectable to 142 $\mu\text{mol L}^{-1}$) and correspondingly the lowest levels of oxygen (undetectable to 164 $\mu\text{mol L}^{-1}$). *Ifremeria nautilei* falls next in the continuum (temperature range: 2.7°C to 32.5°C, sulfide range: undetectable to 129 $\mu\text{mol L}^{-1}$, oxygen range: undetectable to 179 $\mu\text{mol L}^{-1}$), and *Bathymodiolus brevior* is associated with the lowest temperature (2.4°C to 32°C) and sulfide concentrations (undetectable to 84 $\mu\text{mol L}^{-1}$) and the highest oxygen concentrations (undetectable to 180 $\mu\text{mol L}^{-1}$; Podowski et al. 2010). Lab experiments have shown the tolerances of these animals to heat, anoxia, and sulfide generally correspond with their realized distributions (Henry et al. 2008). The analysis of Podowski et al. (2010) included a site with numerous small chimney structures and shimmering water, indicating a hot, newly formed vent site, which was inhabited largely by *Alviniconcha* spp. and was hypothesized to be a site in an early successional stage. Together these studies prompted the formulation of a successional model for the Lau Basin vent community. We hypothesized that *Alviniconcha* spp. is an early successional species that thrives in newly formed vent sites when conditions are hot and sulfidic. Over years, *I. nautilei* is expected to increase in cover, and as a site cools down and venting decreases, *B. brevior* will dominate and can persist for some time after vent activity has ceased. Eventually, venting will cease altogether and the symbiont-containing mollusks will be replaced by non-vent-endemic deep-sea fauna.

The goal of this study was to test these a priori hypotheses of succession through repeat visits to lava sites and edifice structures. High-resolution images were used to document the fauna at the different sites and the environmental conditions (specifically temperature, sulfide and oxygen concentrations) were also documented through the use of in-situ voltammetry. Imagery within the context of a Geographic Information System has been used for studying hydrothermal vent systems in a number of different vent systems around the world (Tsurumi 1998; Copley et al. 1999; Cuvelier et al. 2011) and has recently been used to study previously relatively unknown systems quickly and non-invasively (Podowski et al. 2009; Fabri et al. 2011). Five of the lava sites were visited three times—in 2005, 2006, and 2009. Two lava sites and seven edifice sites

were first visited in 2006 and then again in 2009. In 2005, physico-chemical measurements were only taken at two of the lava sites—Abe1 and Tu'i Malila (TM). In 2006 and 2009, physico-chemical measurements were taken at all lava and edifice sites. A time span of 3 or 4 yr is not sufficient for studying succession in traditional systems such as old fields and forests. However, in systems as dynamic as hydrothermal vents, the entire series of succession may be documented within this time period (Hessler et al. 1988; Lutz et al. 1994; Shank et al. 1998).

Methods

Imagery and mosaicking—Lava (diffuse flow, $n = 7$) and sulfide edifice (vent chimney, $n = 7$) assessment sites were imaged and surveyed thermally and chemically from three vent fields on the ELSC: Kilo Moana (KM), Tow Cam (TC), and Abe; and one vent field on the VFR: Tu'i Malila (TM; Fig. 1). All work was carried out with the remotely operated vehicle (ROV) *Jason II* aboard the R/V *Melville* in 2005 and 2006 and the R/V *Thomas G. Thompson* in 2009. Assessment sites were chosen that hosted dense faunal assemblages typical of the vent field, and that could be approached by the ROV for imaging and environmental sampling. The two lava sites in KM were 136 m apart, the two in TC were 50 m apart, and the two in Abe were 242 m apart. As per Podowski et al. (2010) and Sen et al. (2013), assessment sites were named with a two-letter acronym for the vent field followed by a sequential number. In the case of the Abe vent field, the entire name was used. Edifices additionally had the letter 'C' in the name to represent 'chimneys.' Markers were deployed at each site during the first visit in 2005 (KM1, TC1, ABE1, ABE2, and TM1) or in 2006 for KM2 and TC2 and all edifice assessment sites (KM1C, TC1C, ABE1C, ABE2C, ABE3C, TM1C, and TM2C), and the same heading was maintained while imaging the sites during successive visits.

Images of each assessment site were collected with a digital still camera as per Podowski et al. (2009, 2010) for lava assessment sites and as per Sen et al. (2013) for edifice assessment sites. In short, a series of overlapping pictures was taken with a down-looking camera for lava assessment sites and a forward-looking camera for edifice assessment sites. One set of images was taken at ~ 5 m altitude with the Pixelfly camera, which is a lower resolution camera with high dynamic range that can transfer images to the ship in real-time. These images were downloaded immediately and mosaics of the entire lava site or edifice were constructed while the ROV was still on the seafloor. A customized Matlab program was used for the construction of the mosaics (Pizarro and Singh 2003). Large printouts of these real-time mosaics were made onboard the ship and points were drawn onto the mosaics where we planned to take physico-chemical measurements during the same dive. We chose these points to both replicate the locations from previous years and to fill data gaps in previous data sets.

In addition to the Pixelfly images, two sets of images were taken with a Nikon Coolpix Insite Scorpio digital still camera for each lava and edifice assessment site. For lavas, one set of images was taken from 2 m above the seafloor,

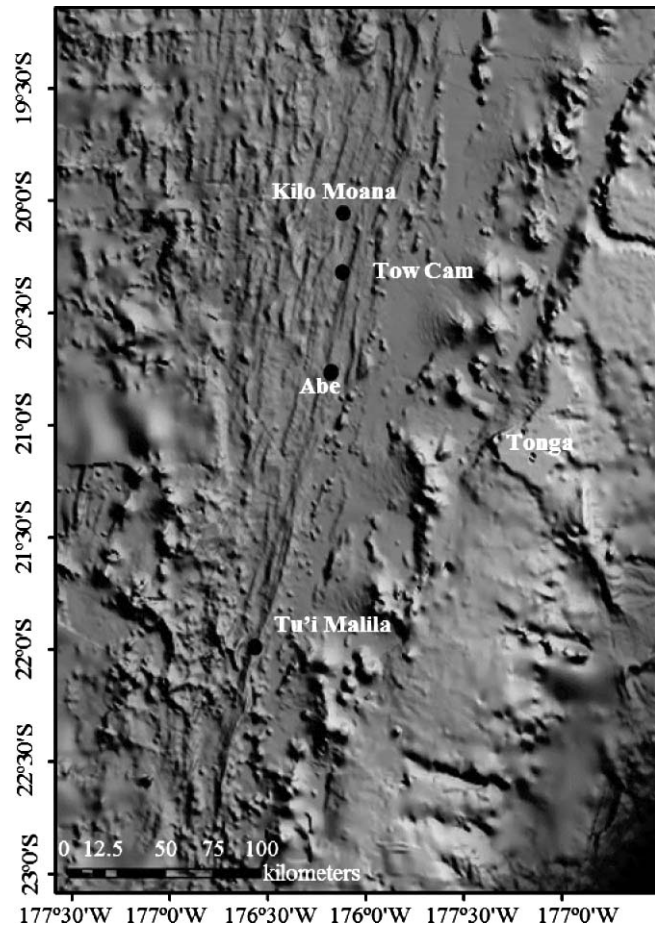


Fig. 1. Hydrothermal vent fields on the Eastern Lau Spreading Center and Valu Fa Ridge.

and the second set was taken 5 m above the seafloor. In 2006, due to practical time constraints, only one set of images was taken for TC2 and KM2 at an intermediate distance of 3 m above the seafloor. The set of images collected from 5 m altitude was used for constructing high-quality photomosaics of each site and the closer set of images was used for identifying and digitizing visible fauna. The images taken from 3 m above the seafloor were of a manageable size for mosaic construction and also provided sufficient resolution for faunal identification. In the case of edifices, two sets of images were also taken at different distances ~ 2 m and ~ 5 m from the edifices; however, the exact distance from the edifices is not known. Similar to the lava sites, the set of images taken from a farther distance was used for constructing high-quality mosaics of the entire edifice and the closer set was used for identifying and digitizing fauna.

Georeferencing—The ROV's navigation data were used to georeference lava sites in the first year the site was visited (procedure described in Podowski et al. 2009, 2010). The photomosaics were imported into ArcMap 9.0 and georeferenced in the World Geodetic System 1984 Universal Transverse Mercator 1 South coordinate system using the navigation data associated with the images. In

subsequent visits to a site, navigation data associated with the pictures constituting the mosaics were recorded but not used to georeference mosaics made that year. Independent navigation data from different years did not correspond exactly with each other, and mosaics georeferenced with their associated navigation data did not line up with the precision necessary for our analyses. The purpose of this study was to examine changes in sites that often occurred at the scale of centimeters; therefore, mosaics from later visits were referenced to the original mosaics. To accomplish this, the later mosaics were imported into ArcMap 9.0 or 10.0 along with the original georeferenced mosaic, and a number of features common to the original mosaic and the newly constructed one were marked. Only rock features were marked, because they did not move in the time span during which this study was conducted. Five or six of these features were linked from the later mosaic to the original mosaic to georeference the later mosaic. The features used were spread evenly throughout the mosaic and different combinations of points were tested to determine the combination that resulted in the least distortion and the best overlap. Because of small differences in altitude and the exact positions of the imaging lines between visits, some distortion and/or inaccuracy in overlap was inevitable, but was on the order of at most a few centimeters. When this was noticeable, changes in these portions of the mosaics were conservatively interpreted. The root mean square error was noted after each georeferencing procedure that provided a numerical estimate of the amount of distortion. This method produced mosaics with generally excellent spatial correspondence between visits and allowed changes at the scale of centimeters to be quantified at most sites. The areas mosaicked in different years were not identical, but only overlapping areas mosaicked in ≥ 2 of the yr were used for temporal change analyses.

In 2006, when the edifices were imaged for the first time, a special coordinate system was created for georeferencing these vertical structures as described in Sen et al. (2013). The 2009 mosaics were georeferenced to 2006 mosaics based on features that were clearly visible in both mosaics as described above for the lava assessment sites. Two edifices changed dramatically between visits; one grew vertically and the top half of another collapsed between 2006 and 2009. However, despite large structural changes, the lower portions of these edifices were nonetheless comparable between years and it was possible to georeference them to one another. Analysis of temporal change of the communities on these edifices were conducted in two ways. The first included only the area in common between the 2 yr in which the edifices were surveyed. Therefore, new vertical growth and the portion that collapsed were not included in this assessment of temporal change. The other approach compared the communities present on the entire edifice, which resulted in total surface areas being different between the 2 yr of study.

Digitization of fauna—The highest resolution set of images from each site was used for identifying and digitizing fauna within ArcMap. Fauna > 2 cm in length or diameter were consistently identifiable using these

images. The symbiont-containing mollusks, barnacles, and colonial zoanthid anemones were all digitized as polygon layers where aggregations were traced, because individuals are difficult to distinguish. Though a number of different *Alviniconcha* species exist, the entire group was treated as a single taxon for the purpose of this study because of the difficulty of distinguishing the different species through imagery alone. There are at least three different orders of barnacles in the Lau Basin that are also indistinguishable from one another in our images; therefore, all non-stalked barnacles were treated as a single group. The zoanthids have not been taxonomically described, and it is not known if one or multiple species occur in the ELSC–VFR, so they were also treated as a single taxon.

Individuals of all other visible fauna were digitized as point layers. When possible, identifications were made to the species level. The animals that could be routinely and reliably identified to the species level were the stalked barnacle *Vulcanolepas* sp.; the squat lobster *Munidopsis lauensis*; the anomuran crab *Paralomis hirtella*; the snails *Enigmaticolus desbruyeresi* and *Phymorhynchus* sp.; the holothurian *Chiridota hydrothermica*; the zoarcid fishes *Thermarces* sp. and *Thermobiotus mytilogeiton*; the polynoids *Branchinotogluma segonzaci*, *Branchinotogluma trifurcus*, *Branchinotogluma* sp. nov., *Harmothoe* sp., *Thermopolynoe branchiata*, and *Levensteiniella raisae*; and the orange anemone *Chondrophellia orangina*. Because species of brachyuran crabs, shrimp, and some anemones could not be reliably distinguished, digitization of each of these taxa included more than one species. The brachyuran crabs *Austinograea williamsi* and *A. alayseae* were digitized as *Austinograea* spp. The taxon ‘shrimp’ could include *Alvinocaris komaii*, *Lebbeus* sp., *Chorocaris vanderavae*, and *Nautilocaris saintlaurentae*. The non-orange anemones known to occur in the Lau Basin—*Cyananthea hourdezi*, *Alvinactis chessi*, *Sagartiogeton erythraios*, *Amphianthus* sp., and an Actinostolidae (Zelnio et al. 2009)—could not be distinguished and were digitized collectively as ‘anemones.’

In situ physico-chemical measurements—An in situ voltammetry wand with a thermocouple was used for measuring temperature, as well as sulfide and oxygen concentrations, at a number of discrete locations at each assessment site (Luther et al. 2000, 2008; Podowski et al. 2009). At each discrete location, 4–7 voltammetric scans were taken, providing a range of temperature and concentration measurements at each location from which maximum, minimum, median, and average temperatures and concentrations could be calculated. The minimum detectable and quantifiable concentration of sulfide was $0.2 \mu\text{mol L}^{-1}$. Undetectable sulfide was treated as half the detectable concentration ($0.1 \mu\text{mol L}^{-1}$) as per Podowski et al. (2009, 2010) and Sen et al. (2013). The minimum detectable concentration of oxygen was $5 \mu\text{mol L}^{-1}$, and the minimum quantifiable concentration of oxygen was $15 \mu\text{mol L}^{-1}$. Consistent with Podowski et al. (2009, 2010) and Sen et al. (2013), half the minimum detectable concentration ($2.5 \mu\text{mol L}^{-1}$) was used for points with undetectable oxygen, and points with detectable but not

Table 1. Summary of the type of data collected from the lava sites in each year of sampling. Edifices were only visited in 2006 and 2009 and in each visit were surveyed both physico-chemically and through imagery.

Site	2005	2006 and 2009
KM1	imagery only	imagery and physico-chemistry
KM2	not surveyed	imagery and physico-chemistry
TC1	imagery only	imagery and physico-chemistry
TC2	not surveyed	imagery and physico-chemistry
ABE1	imagery and physico-chemistry	imagery and physico-chemistry
ABE2	imagery only	imagery and physico-chemistry
TM1	imagery and physico-chemistry	imagery and physico-chemistry

quantifiable oxygen concentrations were treated as the average of detectable and quantifiable limits ($10 \mu\text{mol L}^{-1}$) for statistical analyses. In 2006, a number of temperature measurements were taken with the ROV's temperature probe in addition to measurements taken with the voltammetry wand, because the ROV's probe can withstand higher temperatures than the voltammetry wand, which had a maximum exposure limit of $\sim 60^\circ\text{C}$. In the first year a site was visited, locations where measurements were taken were chosen haphazardly with the aim of covering a diverse array of habitats, including all the aggregated fauna as well as bare substrate that appeared to be exposed to both high and low levels of venting based on the presence or absence of shimmering water. In subsequent visits to the sites, the locations where physico-chemical measurements had been made at a site previously were marked on the new mosaics as described earlier, and we attempted to duplicate these measurements. Locations where measurements were taken during prior visits to the site were identified based on rock features or other non-motile landmarks such as the site markers. Because of coverage by motile fauna, presence of shimmering water, and differences in ROV landing sites, it was often impossible to relocate a measurement precisely. However, our method enabled us to obtain replicate measurements within at most 10 cm of those obtained in previous years. It should be noted, however, that because the focus was on duplicating measurements from previous visits, no measurements were taken on new growth on edifices or on new aggregations of fauna that appeared in later visits. Local ambient temperature was calculated each year at each vent field based on the ROV's conductivity-temperature-depth data. Ambient temperature was subtracted from raw temperatures to obtain the measured temperature anomaly resulting from input of vent fluid, and this was used in statistical tests. In 2005, only ABE1 and TM1 were surveyed physico-chemically. In 2006 and 2009, physico-chemical data were collected from all the lava and edifice sites. Table 1 summarizes the data obtained from each site in the different years.

Statistical and spatial analyses—An important goal of this study was to document change in both the communities

as well as the environmental conditions, and to assess whether changes in one could be linked to changes in the other. Therefore, it was necessary to determine whether an assessment site had experienced a general increase or decrease in venting or whether the overall conditions remained the same. Though attempts were made to duplicate locations where physico-chemical measurements were taken in successive visits to an assessment site, the practicalities of work with ROVs in this environment prevent exact spatial duplication of all measurements, and furthermore, the location of point sources of fluid emission at a site sometimes changed between visits. In order to partially compensate for the bias derived from simple averages of the point measurements made each year, we devised a method for characterizing the overall thermal conditions at a site based on heat maps created from the physico-chemical data (spatially integrated average conditions). For each assessment site, an inverse-distance weighted interpolation of the measurements of maximum temperature at each point was conducted within ArcGIS in order to create a heat map for the entire assessment site. Seven categories of temperature anomaly range were created from this heat map: $0\text{--}5^\circ\text{C}$, $5\text{--}10^\circ\text{C}$, $10\text{--}15^\circ\text{C}$, $15\text{--}20^\circ\text{C}$, $20\text{--}25^\circ\text{C}$, $25\text{--}30^\circ\text{C}$, and $> 30^\circ\text{C}$. The proportion of the area of each site associated with each temperature range was then calculated. Each proportion was multiplied by the mid-point in that temperature range and all areas were summed to obtain a spatially integrated estimate of the average thermal conditions at a site in a given year. A temperature of 35°C was used as the mid-point for the $> 30^\circ\text{C}$ temperature range. For example, if 5% of a particular lava site was associated with temperatures in the range of $15^\circ\text{C}\text{--}20^\circ\text{C}$ and the other 95% associated with temperatures of $5^\circ\text{C}\text{--}10^\circ\text{C}$, 0.05 was multiplied by 17.5°C and 0.95 multiplied by 7.5 and added to obtain a spatially integrated average site temperature of 8°C .

The spatially integrated site averages were compared with the same values obtained in different years in order to ascertain whether sites were generally warmer, cooler, or had remained the same. The differences in these values between visits were compared both absolutely and as a percentage of the value obtained in the earlier year.

This method for characterizing the thermal conditions at a site and assessing changes in these conditions was only applied to the lava assessment sites, because the interpolations are based on the assumption that points in space in close proximity to each other are more similar than two points far away from each other, with no directionality among spatial linkages. Podowski et al. (2010) detected spatial autocorrelation in some lava sites; however, on edifices, lateral diffusion of vent fluids is very low compared with vertical transport along the surface. We did not detect any significant spatial autocorrelation among points for any of the physico-chemical measurements on edifices and conclude that heat maps created on edifices by interpolation would not be representative of the actual distribution of temperatures across their surfaces. In addition to calculating spatially integrated site averages, the heat maps were also used in conjunction with the overlying digitized fauna to visualize movement of the

symbiont-containing mollusks in relation to changing local abiotic conditions.

Paired *t*-tests based on measurements of average temperature anomaly taken within 5 cm of each other in the different years of study were analyzed to complement the calculated spatially integrated temperature anomalies and assess changes in overall environmental conditions at each site. However, the majority of measurement pairs could not be confirmed to be within 5 cm of each other and no such pairs were confirmed for the TC1 or TC2 sites because of abundant shimmering water. However, unlike the spatially integrated temperature anomalies, this method was appropriate for analysis of both lava and edifice sites and so was applied to both.

To compare the composition of communities between years, the portions of each assessment site covered by each group of aggregated fauna in each year were queried in ArcMap 9.0 or 10.0. To determine whether the changes in the communities at the different sites were statistically significant, chi-square tests were conducted between the communities present at each site in the different years of study. The community composition in the prior year comprised the expected values, the community composition in a later year was considered the observed values, and we tested for a difference between the two.

We also tested our direction-driven hypothesis of succession through species-specific chi-square tests. If sites cooled down, we expected *Alviniconcha* spp. to decrease in cover. For the mid-successional species, *I. nautili*, we expected to see increases in coverage if conditions did not change, but decreases in coverage if venting declined. We hypothesized that *B. brevior* is the late-successional species and therefore expected to see increases in coverage of this species if conditions did not change or if venting declined. For each of the groups, the number of sites where physico-chemical data were available and the faunal groups were present were the expected frequencies and the number of times the faunal groups changed in the way we expected were the observed frequencies.

The symbiont-containing faunal groups are all mobile; therefore, it is possible that the changes seen at the sites were simply due to relocation and niche partitioning and not succession. In order to test this alternative hypothesis, we examined the sites where the average physico-chemical parameters did not change. If no succession is occurring and the animals are merely moving around in sync with changing fluid exits, then we would not expect the coverage of the different faunal groups to change. We conducted a chi-square test in which the expected frequencies were the total number of sites where environmental conditions did not change and the observed frequencies were the number of those sites where the faunal group coverage did not change. In order to assess whether the overall community at each site changed over time, taxonomic richness and beta diversity within the sites between the different time points were calculated. The temporal beta diversity provided an estimate of the amount of species turnover at each site and was calculated by counting the number of taxa unique to each visit. Temporal beta diversities were calculated based on all two-time-point combinations (i.e., 2005 and 2006,

2006 and 2009, and 2005 and 2009). Beta diversities can be affected by the presence or absence of a taxon represented by a single individual, so Bray–Curtis similarity between the different visits to the each site was also calculated. This similarity index was then subtracted from 100 to obtain a dissimilarity index. The beta diversity and the dissimilarity index together provided complementary methods to characterize species turnover with time.

A regression analysis was conducted with all the physico-chemical measurements acquired in 2006 and 2009, where maximum temperature anomaly was the independent variable and maximum sulfide concentration was the dependent variable. The slopes were compared between the 2 yr to determine whether the sulfide:temperature ratio in the vent fluid had changed between years.

The temperatures, sulfide concentrations, and oxygen concentrations associated with the five groups of aggregated fauna were compared through multiple Mann–Whitney tests in order to assess whether or not the environmental conditions associated with the faunal groups changed over time. Multiple tests were conducted; therefore, a sequential Bonferroni correction method was used to adjust the alpha value and correct for the different tests (Holm 1979).

Results

Changes in lava sites—The comparison of all spatially integrated temperature data from the lava sites between years suggests that the surveyed region may have cooled a small amount (0.6°C on average) between 2006 and 2009 (the only interval when data were available for all vent fields). Over this time period, the overall coverage of *Alviniconcha* spp., barnacles, and zoanthids increased. The overall increase in coverage by *Alviniconcha* spp. is driven by a large increase in this faunal group at one site—TC2.

Based on the paired *t*-tests, a significant change in overall temperature occurred only at one site—KM1 (Table 2). The absolute magnitude of change in the spatially integrated average temperature anomalies at each site was < 2.5°C, although the percent change in the temperature anomaly was > 25% at three of the sites, suggesting a substantial change in the average conditions at these sites but not the others (Table 3). The biggest change was observed at KM1, where there was a 92% decrease in temperature from an average of 2.5°C above ambient to only 0.2°C above ambient between 2006 and 2009. Average temperatures at ABE2 also cooled between 2006 and 2009, from 3.6°C above ambient to 2.6°C above ambient, a reduction of 28%. The average temperature at TM1 increased between 2005 and 2006 by 33% from 4.2°C to 5.6°C above ambient. The integrated average change (either increase or decrease) at all other sites was ≤ 1°C and represented ≤ 10% of the absolute temperature.

Consistent with the large decrease in average temperature, one of the most dramatic changes in fauna was at KM1 (Fig. 2). In 2005, *I. nautili* and *B. brevior* were both present at this site. A year later, in 2006, most of the snails had disappeared, while the mussels showed a small increase in their areal coverage, and there was a large increase in the area covered by zoanthids. By 2009, *I. nautili* was absent

Table 2. Results of paired *t*-tests for average temperature at each site between years of study. Paired samples were not available for the TC1 and TC2 lava sites.

Lava site	Study years	Mean difference	<i>n</i>	<i>p</i> -value	df	Edifice site	Study years	Mean difference	<i>n</i>	<i>p</i> -value	df
KM1	2006–2009	−2.0	11	0.045	10	KM1C	2006–2009	0.2	8	0.802	7
KM2	2006–2009	−0.3	11	0.861	10	TC1C	2006–2009	1.5	7	0.166	6
ABE1	2006–2009	3.7	8	0.161	7	ABE1C	2006–2009	−7.9	6	0.294	5
ABE1	2005–2006	8.7	9	0.275	8	ABE2C	2006–2009	−6.0	6	0.329	5
ABE2	2006–2009	−1.9	7	0.133	6	ABE3C	2006–2009	−1.5	4	0.069	3
TM1	2006–2009	3.8	8	0.109	7	TM1C	2006–2009	−4.6	6	0.235	5
TM1	2005–2006	1.42	9	0.222	8	TM2C	2006–2009	4.9	4	0.142	3

from the site, the mussel coverage decreased slightly, and zoanthid coverage continued to increase from an initial coverage of 0.4% to a final coverage of 16%. The change in the coverage of the symbiont-containing mollusks was statistically significant between both 2005 and 2006 as well as between 2006 and 2009 (Table 4).

A similar pattern of decline in *I. nautili* with a parallel increase in mussels was documented at ABE2, the other site where a substantial decrease in the spatially integrated average temperature anomaly was detected. In 2005, the coverage of aggregated fauna at ABE2 was dominated by *I. nautili*, and 1 yr later the coverage of *B. brevior* and *I. nautili* were about equal, although the change in coverage of the symbiont-containing mollusks was not statistically significant between 2005 and 2006 (Table 4). By 2009, when the spatially integrated temperature anomaly had decreased by 28% from 2006, mussels dominated the aggregated faunal coverage and the change in cover of the symbiont-containing mollusks was statistically significant (Fig. 2; Table 4).

Though no substantial differences in the environmental conditions between visits were detected at TC2 or KM2, there were important changes in faunal coverage at these sites. At TC2, the cover of *Alviniconcha* spp. and *I. nautili* increased, and *B. brevior* appeared between 2006 and 2009 and the coverage of the symbiont-containing fauna was statistically different (Fig. 2; Table 4). At KM2, the coverage of the symbiont-containing mollusks changed

significantly (Table 4). Increases in the area covered by zoanthids and barnacles also occurred (Fig. 2) and although not apparent in the summary data, a small but notable increase in the cover of *I. nautili* occurred in 2009 through establishment of aggregations in areas that had been devoid of symbiont-containing fauna in 2006. *B. brevior* appeared to move into multi-layered clumps with an apparent decrease in area cover. The overall coverage of the aggregated fauna at the three other sites was not statistically different over the 2005–2009 time period. However, small changes in the coverage of the individual faunal groups occurred, and according to the chi-square tests, the number of times changes occurred at these sites was statistically different from the null hypothesis of no changes in fauna at these sites as expected through niche partitioning alone ($p = 0.0009$). For example, increases were seen in *B. brevior* at all of these sites (Fig. 2).

None of the changes among the symbiont-containing mollusks were statistically different from the expected directional change in these faunal groups based on our succession hypotheses ($p = 0.5403$ for *Alviniconcha* spp., $p = 0.4483$ for *I. nautili* and $p = 0.4795$ for *B. brevior*).

Taxonomic richness (alpha diversity) ranged from 7 to 12 taxa across all lava assessment sites in all years (Table 5). The lowest taxonomic richness was recorded at TC2 in 2006 and 2009 and TM1 in 2005. The highest taxonomic richness—12 taxa—was recorded at KM1 in 2005 and KM2 in 2006. The highest temporal beta

Table 3. Spatially integrated temperature anomalies at each lava site by year. Change from 1 yr of study to another is expressed in terms of absolute differences as well as in terms of a percentage of the spatially integrated temperature anomaly calculated in the earlier year of study. All sites were surveyed thermally in 2006 and 2009. Only ABE1 and TM1 were surveyed thermally in 2005; therefore, 2005–2006 comparisons could only be made for these two sites.

Site	Average temperature anomaly in 2006	Average temperature anomaly in 2009	Change in average temperature anomaly	Change as percent of 2006
KM1	2.5	0.2	−2.3	−92
KM2	1.4	1.4	0.0	0.0
TC1	5.2	5.3	0.1	1.9
TC2	4.7	5	0.2	4.2
ABE1	8.5	7.9	−0.6	−7.1
ABE2	3.6	2.6	−1.0	−27.8
TM1	5.6	5.2	−0.4	−7.1
2005 to 2006	Average temperature anomaly in 2005	Average temperature anomaly in 2006	Change in average temperature anomaly	Change as percent of 2005
ABE1	7.7	8.5	0.8	10.4
TM1	4.2	5.6	1.4	33.3

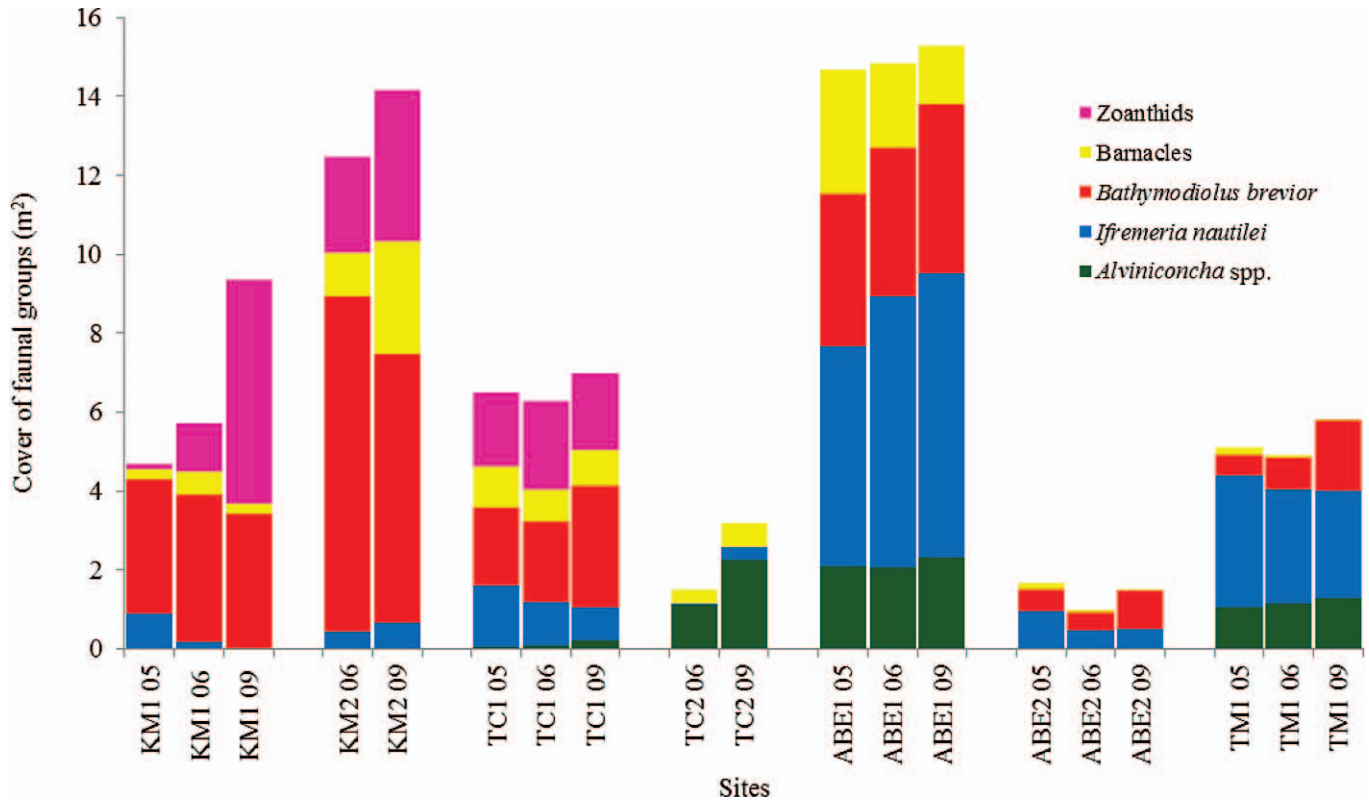


Fig. 2. Areas covered by the aggregated faunal groups at the lava sites in each year of study.

diversities were recorded at KM1, and the lowest were recorded at TM1 and TC1. There were no differences in the diversity indices between sites or years. The highest and lowest beta diversities and dissimilarity indices between visits were recorded consistently at KM1 and TC1, respectively (Table 5).

Changes in edifice sites—Interpolation was deemed inappropriate for estimation of spatially integrated average temperatures on edifices, so we assessed average changes in temperatures based on the paired *t*-tests. No significant changes in thermal conditions were observed at any of the edifice sites (Table 2), but the paired *t*-tests did not take into account new sources of venting or vertical growth on edifice structures. The edifices were originally chosen for study because of the presence of aggregated fauna on them in 2006, and all edifices still hosted aggregated fauna in 2009. All of the aggregated faunal groups present on lavas except zoanthids were also present on edifices. Edifices generally hosted more individuals and species of polynoids than lava sites, and only one seemingly old edifice hosted the sea cucumber *Chiridota hydrothermica*, which was present in a number of lava sites. Five of the seven edifices were structurally similar in both years. ABE1C experienced vertical growth of ~ 1.2 m, adding an area of 0.46 m² to the two-dimensional mosaic for this edifice, which indicated more hydrothermal activity through this edifice than any other. However, the overall aggregated faunal cover did not change significantly (Table 4). The faunal coverage on the

portion present in both years decreased because of the absence of *Alviniconcha* spp. on old portions of the edifice. Although barnacle coverage increased on old portions of the edifice, none were observed on the new growth where *I. nautiliei* dominated the aggregated fauna category (Fig. 3).

The top portion of ABE3C collapsed, thereby reducing the height of this edifice from 3.3 m to 2.7 m and resulting in a 0.17 m² decrease in two-dimensional area of the edifice mosaic. This narrow edifice went from a sparse cover that included both snails and mussels in 2006 to a sparse cover of largely *B. brevior* in 2009 (Fig. 4), though the change in the community was not statistically significant (Table 4).

The TM1C edifice was stable in terms of both its structure and the aggregated faunal community in both years that it was imaged. However, edifices are generally dynamic, and in addition to major structural changes, new sources of venting can open up on the surface of the structures, which can very quickly affect the composition of the communities present on the edifice. For example, on KM1C, two cracks about halfway up the structure became active between visits (Fig. 5). In 2006, one crack was devoid of aggregated fauna and the other hosted a small aggregation of *B. brevior*. In 2009, the areas around these cracks were dominated by aggregations of *I. nautiliei* with a few individuals of *B. brevior*. White substrate is also clearly visible in one of these cracks in 2009, which is likely either newly formed anhydrite or reflects bacterial activity. This was accompanied by an overall increase in both barnacles and *I. nautiliei* on the structure (Fig. 5). The top portion of

Table 4. Results of chi-square tests for differences in symbiont-containing mollusk coverages for each lava assessment site.

		2005–2006	<i>p</i> -value	2006–2009	<i>p</i> -value
Lava sites					
KM1	fauna significantly different		0.0014	fauna significantly different	7.05×10^{-05}
KM2	na		na	fauna significantly different	0.0419
TC1	fauna not significantly different		0.6064	fauna not significantly different	0.3454
TC2	na		na	fauna significantly different	0.0275
ABE1	fauna not significantly different		0.4241	fauna not significantly different	0.5678
ABE2	fauna not significantly different		0.5510	fauna significantly different	0.0281
TM1	fauna not significantly different		0.5926	fauna not significantly different	0.2682
Edifice sites					
KM1C	na		na	fauna significantly different	4.88×10^{-39}
TC1C	na		na	fauna not significantly different	0.6781
ABE1C	na		na	fauna not significantly different	0.5084
ABE1C (common area)	na		na	fauna not significantly different	0.4666
ABE2C	na		na	fauna not significantly different	0.1479
ABE3C	na		na	fauna not significantly different	0.8333
ABE3C (common area)	na		na	fauna not significantly different	0.7969
TM1C	na		na	fauna not significantly different	0.8963
TM2C	na		na	fauna not significantly different	0.7138

the edifice appeared to cool down slightly, which is indicated by a small reduction in visible white substrate. Fifteen measurements were taken on the top-most portion of the edifice in 2006 and seven were taken in 2009. The mean of the average temperature anomalies recorded in this region was 0.8°C in 2009, which is a reduction of 1.6°C.

The coverage of mussels also decreased in this area, from 0.9858 m² to 0.8071 m². As a whole, the community on this edifice changed significantly from 2006 to 2009 (Table 4). TC1C and ABE2C are two other examples of edifices that did not change structurally but experienced notable (but not statistically significant) changes in the communities.

Table 5. Taxonomic richness (alpha diversity) in each study year, and temporal beta diversities and Bray–Curtis dissimilarity indices of all lava sites between years.

	Alpha diversity			2005 to 2006		2006 to 2009		2005 to 2009	
	2005	2006	2009	beta diversity	dissimilarity	beta diversity	dissimilarity	beta diversity	dissimilarity
Lava site									
KM1	12	9	10	4	23	7	24	9	35
KM2	—	12	9	—	—	3	11	—	—
TC1	10	11	10	1	4	1	4	2	6
TC2	—	7	7	—	—	4	17	—	—
ABE1	10	11	10	3	7	3	9	3	13
ABE2	8	10	8	4	15	2	8	3	18
TM1	7	9	9	2	12	0	7	2	18
Edifice site									
KM1C	—	14	12	—	—	3	25	—	—
TC1C	—	9	8	—	—	5	16	—	—
ABE1C	—	13	11	—	—	4	16	—	—
ABE1C (common area)	—	13	11	—	—	5	21	—	—
ABE2C	—	14	11	—	—	6	12	—	—
ABE3C (common area)	—	11	7	—	—	4	39	—	—
ABE3C	—	11	7	—	—	4	41	—	—
TM1C	—	7	8	—	—	4	18	—	—
TM2C	—	11	9	—	—	6	38	—	—

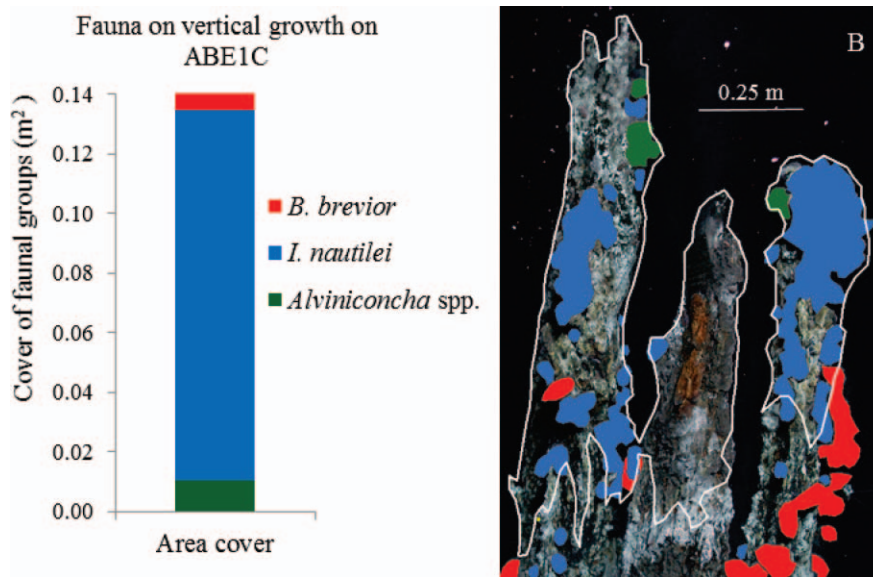


Fig. 3. Fauna on new vertical growth on the ABE1C edifice from 2009. (A) The stacked column graph shows the coverage of the different aggregated faunal groups on the new growth. (B) An image of the growth (outlined in white) is shown with the aggregated fauna digitized on the structure.

Both *Alviniconcha* spp. and *B. brevior* decreased on TC1C, and barnacles increased (Fig. 4). On ABE2C, *Alviniconcha* spp. and *I. nautiliei* increased, while *B. brevior* decreased.

The taxonomic richness of visible fauna on edifices varied from 7 to 14, in the same range as at the lava sites (Table 5). Temporal beta diversities on edifices ranged from three to six between 2006 and 2009, compared with lava sites, which ranged from zero to seven in this time frame (Table 5). Dissimilarity indices were consistently higher among edifices than lava sites and ranged from 12 on ABE2C to 41 on the ABE3C edifice, compared with a range of 4 to 24 for lava sites between 2006 and 2009. For edifices that changed structurally (ABE1C and ABE3C), there was not a large difference in beta diversity or the dissimilarity index when comparing both the areas in common in both years, or when comparing the entire structures (Table 5).

Changes in animal habitats and diffuse-flow sulfide: Temperature ratios between visits—There was no significant change in the average concentration of sulfide associated with any group of aggregated fauna between 2006 and 2009 (Fig. 6A). The average temperature measured with *B. brevior* and *I. nautiliei* was lower in 2009 than 2006 ($p < 0.0001$ and $p = 0.0048$, respectively) but does not differ between the 2 yr of study for any of the other faunal groups (Fig. 6B). However, the average concentration of oxygen measured in association with *I. nautiliei*, *B. brevior*, barnacles, and zoanthids was significantly lower in 2009 than 2006 ($p = 0.0017$, $p = 0.0063$, $p = 0.005$, and $p = 0.001$, respectively; Fig. 6C). Because oxygen and sulfide co-vary inversely in diffuse flow and because zoanthids are present in water with almost no temperature anomaly, these data suggest the difference in oxygen concentration within animal habitats reflects

differences in the background bottom-water oxygen content between visits.

The sulfide:temperature ratio changed significantly between 2006 and 2009. It was higher in 2009 ($p = 0.00002$), which means that for any given temperature, sulfide concentration of the vent fluid was higher in 2009 than in 2006 (Fig. 7).

Heat maps based on in situ measurements showed that the areas of active venting corresponded very well with animal distributions. Symbiont-containing mollusks clearly avoided areas with ambient conditions and relocated themselves based on changes in venting within an assessment site (Fig. 8).

Discussion

Patterns of succession in Lau Basin vent communities—The Lau Basin provides a unique system for studying successional patterns, because the core species are mobile animals that act as primary producers because of their symbiotic associations with chemoautotrophic bacteria. We hypothesized a model of succession based on the dominant symbiont-containing mollusks in which *Alviniconcha* spp. is the pioneering faunal group that dominates hot, newly formed vent sites. Over time, the mid-successional species *Ifremeria nautiliei* will increase in cover, and as a site begins to cool down, the late-successional species *Bathymodiolus brevior* will dominate and can persist for some time at low levels of vent activity. Overall, our results support our hypothesized model of succession. TC2 represents a site that is likely in an early successional stage, where the fauna is dominated by *Alviniconcha* spp. However, *I. nautiliei* increased considerably over a 3 yr time period at this site and *B. brevior* also started colonizing this site. ABE1 and TM1 represent sites in the next stage, where the different

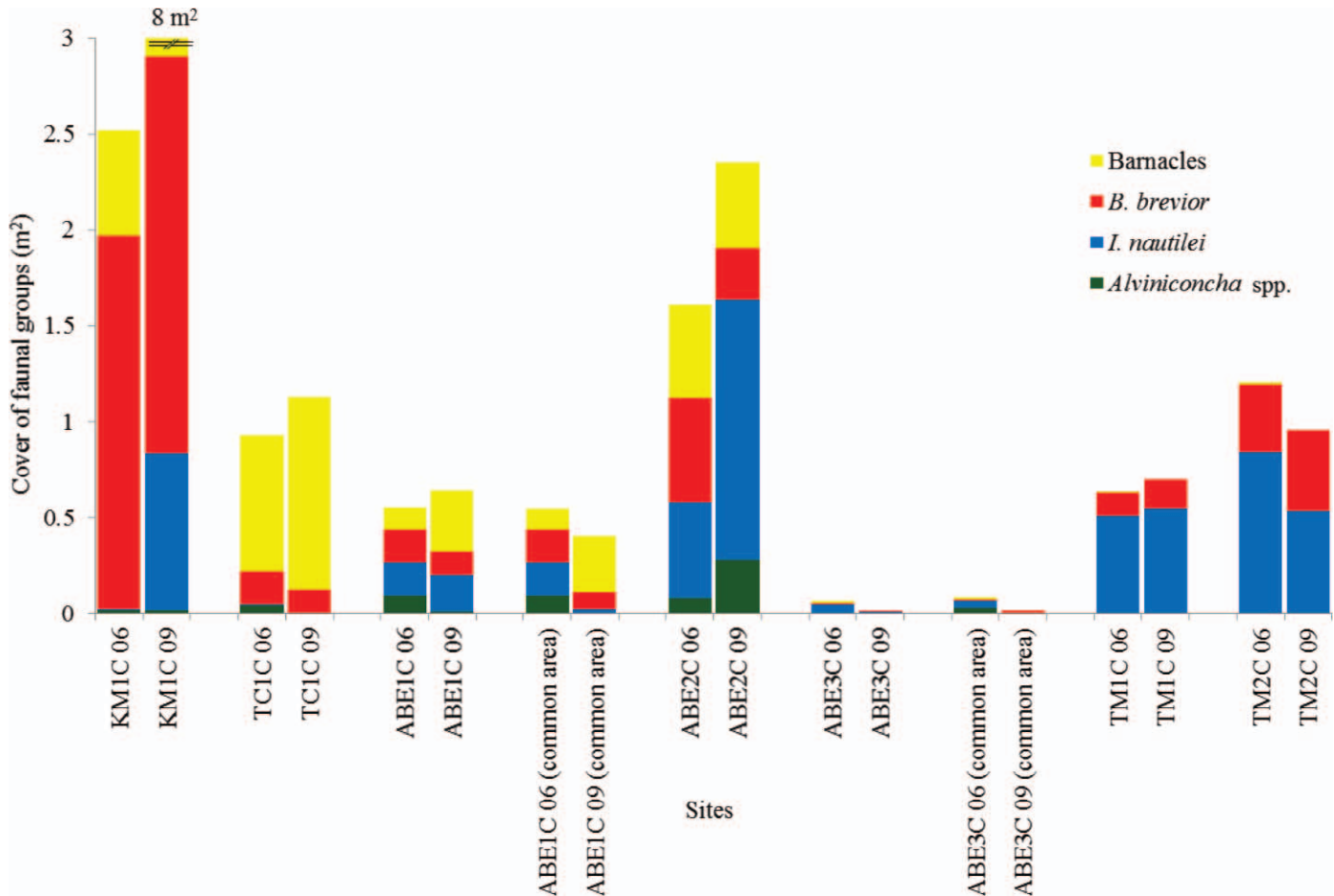


Fig. 4. Areas covered by the aggregated faunal groups at the edifices in the 2 yr of study. The column for KM1C reaches $\sim 8 \text{ m}^2$ in total with barnacles.

symbiont-containing faunal groups are present, but *I. nautiliei* is the dominant faunal group. TC1 is similar to these sites, but is slowly progressing to the next stage as is seen by the slow decline in *I. nautiliei* and increase in *B. brevior* at this site. A complete transition to the next stage of dominance by *B. brevior* is clearly seen at the KM1 site, where, by 2009, both *I. nautiliei* and *Alviniconcha* spp. have disappeared and *B. brevior* is the only symbiont-containing faunal group present. A similar transition appears to be occurring at the ABE2 site, where *I. nautiliei* was the dominant symbiont-containing faunal group in 2005, but 4 yr later, in 2009, *B. brevior* was the dominant faunal group at the site.

Because this study captured sites at different stages of succession, and we observed the progression of these sites over time, we were able to expand upon this hypothesis in our characterization of succession in Lau Basin vent communities. For example, zoanthids increased in cover at sites where venting decreased (Fig. 2; KM1 and KM2), and because they are associated with near-ambient conditions and are not known to harbor sulfide-oxidizing symbionts, we believe they represent a penultimate stage of vent community succession in this region and can persist at a site after the disappearance of other vent fauna. However,

this stage in the successional sequence likely only occurs in the northern, basalt-hosted sites because, zoanthids are rare in the southern, andesite-hosted sites (Podowski et al. 2010).

Among the aggregated fauna, an actual addition or disappearance of species only occurred when environmental conditions changed and sites cooled down (e.g., KM1 where *I. nautiliei* declined and then disappeared, and *Alviniconcha* spp. disappeared; Fig. 2) or in early successional stages, where later successional species apparently have not arrived yet (appearance of *B. brevior* at TC2; Fig. 2). ABE2 is another site where temperature and sulfide concentrations are declining, and though no disappearance of aggregated fauna has occurred yet at this site, *I. nautiliei* has been consistently decreasing and *B. brevior* has been increasing in cover over time. At sites where environmental conditions remained the same, and even when a site warmed up (e.g., TM1), no turnover of aggregated fauna occurred, but later successional species increased in cover over time. This suggests that under stable conditions, biological interactions are more important and result in an increase in coverage of later successional faunal groups, even though environmental conditions have a stronger effect when venting changes significantly. Based on colonization experiments in the

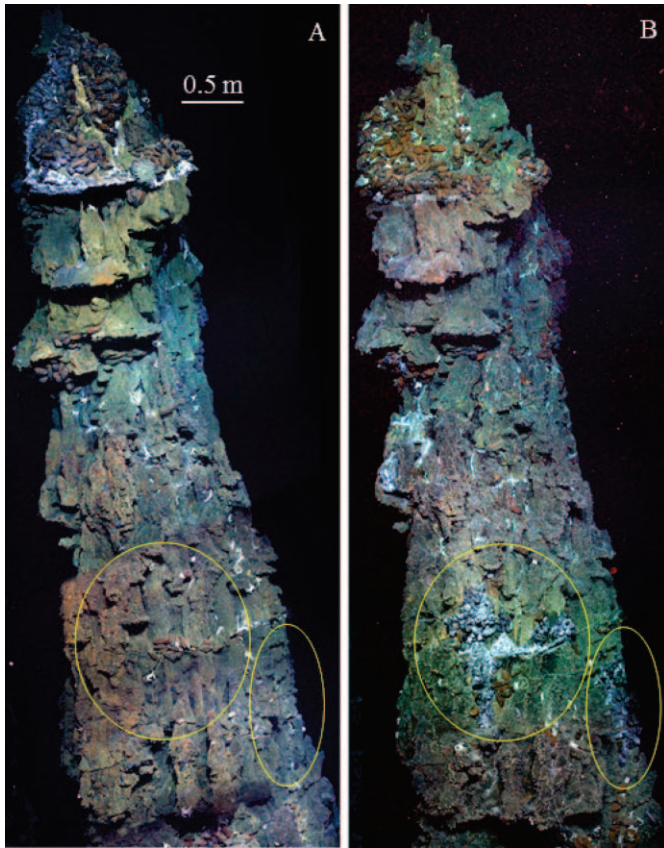


Fig. 5. KMIC edifice in (A) 2006 and in (B) 2009 showing cracks in the structure where new venting appears to have begun, evident from the white coloration of the substrate. Both these new sources of venting are dominated by *Ifremeria nautiliei* snails.

Eastern Pacific, Mullineaux et al. (2003) suggested similar drivers of succession.

Solitary fauna (non-aggregated) that are found only in early and mid-successional stages are the bythograeid crabs *Austinograea alayseae* and *Austinograea williamsi*, which were not seen at sites in later successional stages such as KM1 and ABE2. These crabs were found to be associated with *Alviniconcha* spp. and *I. nautiliei* (Podowski et al. 2010); and related species on the East Pacific Rise (EPR), such as *Bythograea therymydon*, have been found to have high tolerances for heat, high sulfide, and low oxygen (Mickel and Childress 1980, 1982; Dahlhoff et al. 1991). Bythograeid crabs, such as the *Austinograea* species present at these sites, seem well-adapted to take advantage of the high levels of primary production associated with venting, but largely disappear when active venting decreases below a certain level. Shrimp also disappeared or decreased in numbers as sites progressed to later successional stages. Species such as the sea cucumber *Chiridota hydrothermica* and the squat lobster *Munidopsis lauensis* are absent or present in low numbers at sites at early successional stages but are more frequent at sites in later successional stages. Podowski et al. (2010) found these species to occupy areas of little or moderate venting; thus, it is not surprising that they follow the opposite trend of the bythograeid crabs as venting conditions change over time.

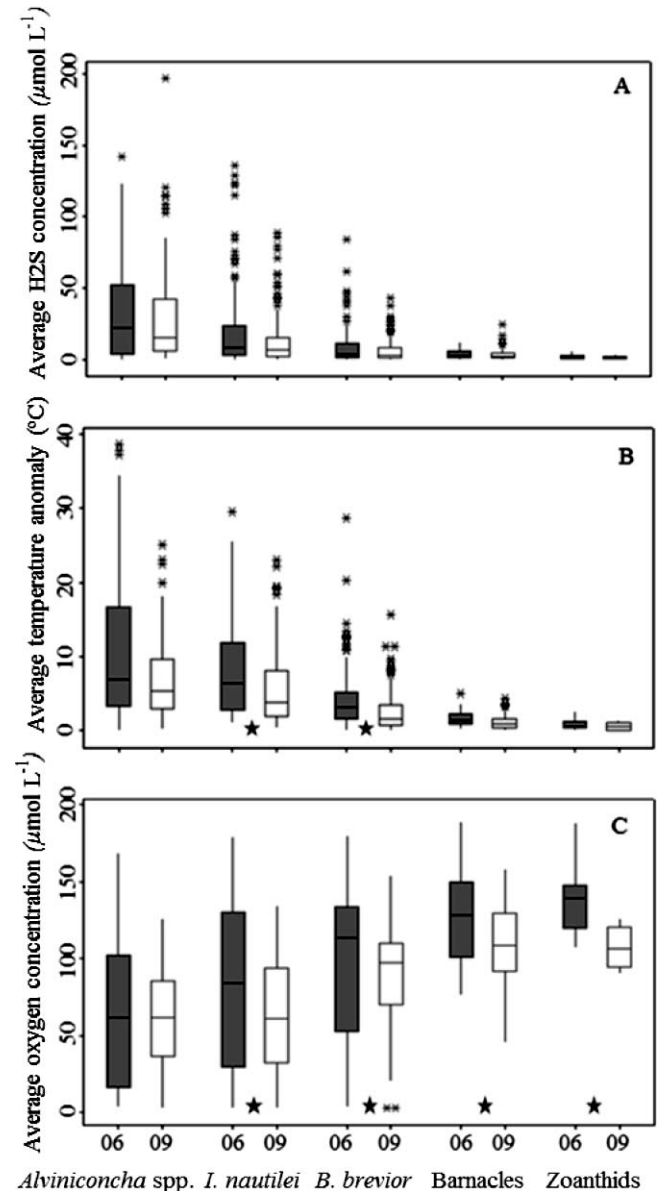


Fig. 6. Box plots showing the physico-chemical environments associated with the different groups of aggregated fauna in 2006 and 2009. The box represents the interquartile range and the whiskers represent the upper and lower limits (defined as the value at $Q3 + 1.5(Q3 - Q1)$ for the upper limit and $Q1 - 1.5(Q3 - Q1)$ for the lower limit). Asterisks above the whiskers represent values that are greater than the value at the upper limit. Asterisks between the years represent significant differences between the years of study. (A) shows average sulfide concentration, which was not significantly different between the 2 yr of study for any of the faunal groups after a sequential Bonferroni correction. (B) shows the average temperature anomaly, which was not significantly different between the 2 yr of study for *Alviniconcha* spp., barnacles, and zoanthids, but was significantly higher in 2006 for *I. nautiliei* ($p = 0.0048$) and *B. brevior* ($p < 0.0001$) after a sequential Bonferroni correction. (C) shows the average oxygen concentration, which was not significantly different for *Alviniconcha* spp., but was significantly higher in 2006 for *I. nautiliei* ($p = 0.0017$), *B. brevior* ($p = 0.0063$), barnacles ($p = 0.005$), and zoanthids ($p = 0.001$) after a sequential Bonferroni correction.

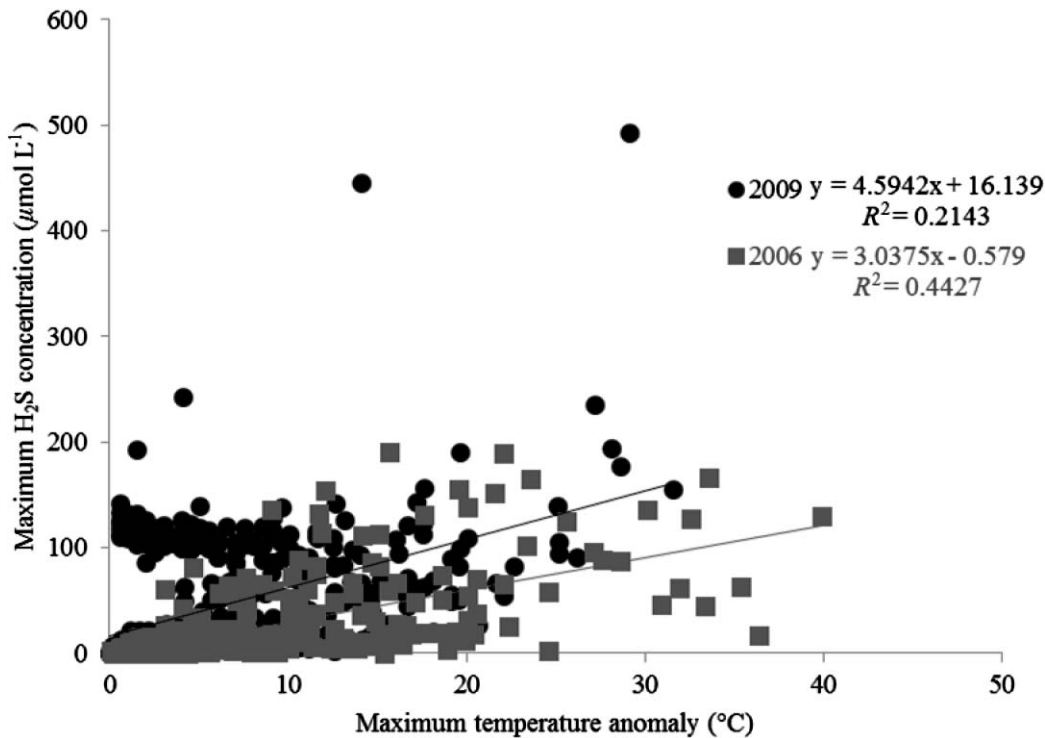


Fig. 7. Sulfide: temperature ratio in 2006 and 2009. The sulfide: temperature ratio is significantly higher in 2009 ($p = 0.00002$).

At KM1, where venting almost completely ceased, non-vent-endemic species such as brisingid sea stars appeared, and corals and sponges were observed at the edges of this site as well. A number of these non-vent-endemic species were observed on old, inactive edifices and therefore represent a final stage of succession at Lau vents on lava and edifice habitats alike.

Species richness and diversity (incorporating evenness) have been shown to increase (Odum 1969) or decrease in late-successional stages (Margalef 1963) or have a bimodal distribution in which middle stages are less diverse than early and late stages (Johnston and Odum 1956). Our results show no substantial change in taxonomic richness at different successional stages (Table 5), although it is important to note that because our methods do not always allow identification to species or even genus level, and the entire range of taxonomic richness within a site was 7 to 12 taxa, there is substantial cryptic diversity we were not able to observe. Podowski et al. (2009) made animal collections at one of the lava assessment sites—ABE1—and found that 22 species could be identified from the animal collections in addition to the taxa that could be observed within the mosaic. However, these additional species only constituted 2% of the estimated total biomass of the community at the ABE1 site. In addition, small associated fauna, often hidden among the large symbiotic mollusks, may also prove more variable from one successional stage to another. However, the beta diversities and dissimilarity indices indicating species turnover do indicate a temporal pattern, being higher in sites where the environmental conditions are changing (KM1 and ABE2) and lower in

sites with relatively stable environmental conditions (TM1 or TC1; Table 5).

A predominant tenet of succession is that pioneering species dominate newly created patches. For example, when a tree falls during a storm, the newly cleared patch brings an opportunity for early successional species to grow in a forest dominated by later successional species. Sarrazin et al. (1997) found that new accretions on edifices in the Juan de Fuca hosted aggregations of the highly heat-tolerant *Paralvinella sulfincola* worms. Therefore, we expected new growth on edifices or new sources of venting to be dominated by *Alviniconcha* spp., the most heat-tolerant of the aggregated faunal groups. As mentioned before, we did not collect environmental data from these locations because our aim was to duplicate environmental data collected on prior visits as closely as possible. The presence of white substrate, as well as shimmering water, indicates that these areas host high temperatures and concentrations of sulfide. Therefore, they are likely within the niche preferences of *Alviniconcha* spp. However, *I. nautiliei* dominated the new vertical growth on the ABE1C edifice and also dominated the areas where new cracks of venting opened along the KM1C edifice. Therefore, at ELSC-VFR vents, the mid-successional species can dominate new substrates or sources of venting where it is already present, probably by movement of adults into new patches rather than recruitment of larvae. However, Reynolds et al. (2010) found that *I. nautiliei* broods embryos, which could confer advantages such as lower juvenile mortality or even the possibility of symbiont uptake within the brood pouch itself and could contribute

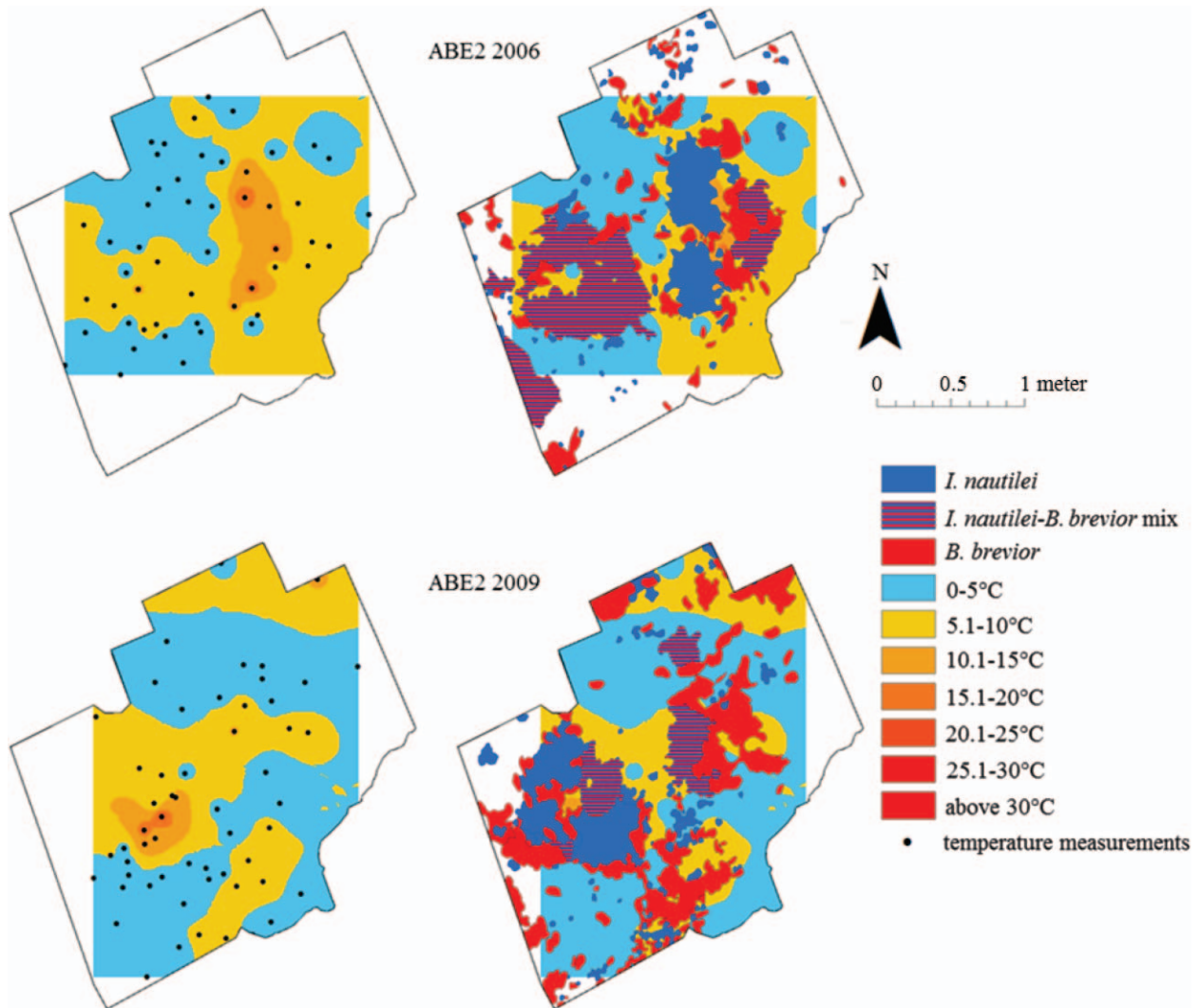


Fig. 8. Heat maps of the ABE2 lava site in 2006 and 2009 using maximum temperature measurements overlaid with the digitized fauna. All measurements at the site in the 2 separate yr were used to construct the heat maps that extended beyond the common perimeter. However, these maps were clipped for this figure to only show the area in common between the 2 yr. For both years of study, the heat maps with the points where measurements were taken are shown on the left and the distribution of the symbiont-containing faunal groups overlain on the heat maps are shown on the right. The hot spot has moved from 2006 to 2009 and the distribution of *I. nautiliei* also changed so that in both years this species is located directly above the hot spot.

to this species' dominance in new substrates and around new sources of venting.

Symbiotic mollusks move to maintain physico-chemical milieu—The symbiont-containing mollusks in the ELSC-VFR each require a certain range of environmental conditions, but instead of simply dying when conditions become unfavorable as do the sedentary fauna in other vent systems and plants in terrestrial systems, the mollusks respond to local changes of vent flow by moving to maintain their location within a certain range of conditions. Our results show that the sulfide:temperature ratio increased from 2006 to 2009 and the sulfide concentrations associated with the different faunal groups did not differ over time even though the location or abundance of the animals within a site may have changed dramatically. The

temperatures associated with *I. nautiliei* and *B. brevior* declined from 2006 to 2009. These results suggest that the symbiont-containing mollusks track sulfide over temperature and maintain themselves in locations with adequate sulfide to fuel their symbiotic partners. Figure 8 shows the rearrangement of the aggregated faunal groups at ABE2 corresponding with the changes in venting. In each year, the bulk of the *I. nautiliei* at ABE2 were located over the hottest area in the site (there were no *Alviniconcha* spp. present in either year), even though the hottest spot changed in location between years. Movement of the faunal groups in order to remain in similar conditions was also seen on edifice structures. For example, on the edifice ABE1C, the middle of the edifice in 2009 is what used to be the top of the edifice in 2006, and *Alviniconcha* spp. moved up to the new top of the edifice where the physico-chemical

conditions had become more suitable. This movement is similar to what has been observed on edifices in the Juan de Fuca where mobile animals such as paralvinellid worms and snails move in response to changing environmental conditions (Sarrazin et al. 1997). However, these animals are not functionally primary producers and, in fact, the symbiont-containing vestimentiferan tubeworms at Juan de Fuca are incapable of moving and although they can tolerate a wide range of conditions, will die, much like plants in terrestrial systems, when conditions are no longer appropriate.

In general, animals regularly move to remain in suitable conditions, such as desert animals moving into the shade during the day and foraging at night (Rewald et al. 2012). However, Western Pacific vent fauna are a rare case in the succession literature in which the core species, which are functionally primary producers, move in response to changing environmental conditions over time. Most studies of animal succession deal with sessile organisms, and therefore, changing local conditions result in species replacements. However, we have shown that changing conditions need not result in species replacement if the animals involved are mobile and suitable habitat is still available within the general area, which could contribute to the overall stability in community composition at these vents. The movement in sync with the realignment of suitable habitats represents a step in the process of succession that can occur concurrently with the replacement and turnover of species within an area. For example, while the symbiont-containing mollusks track changes in vent flow at the ABE2 site, the site as a whole also appears to be cooling down, and the cover of *I. nautiliei* has decreased with each visit (2005, 2006, and 2009), while the cover of *B. brevior* increased over time (Fig. 2). Our tests support the hypothesis of succession; however, because both environmental and biological factors appear to play a role in the successional process in the Lau Basin, one cannot ignore the role of niche partitioning as contributing to the changes in these communities over time.

Stability and longevity of Western Pacific vent communities—Vent communities in the Eastern Pacific are extremely dynamic and can progress through all of the successional stages within only 3–5 yr (Hessler et al. 1988; Shank et al. 1998; Marcus et al. 2009), while vents in the Mid-Atlantic Ridge (a slower spreading system than the EPR) are much more stable (Copley et al. 1999, 2007; Cuvelier et al. 2011). The ELSC–VFR is a fast-spreading system similar to the EPR, so Lau vents were expected to be dynamic-like vents in the Eastern Pacific. However, a number of sites (ABE1, TM1, TC1) appear to be relatively stable over a period of 4 yr. Edifices also appear to be structurally stable in comparison with the highly dynamic edifices found on the Juan de Fuca Ridge (Tunnicliffe and Juniper 1990), and only two of the six included in this study either grew or collapsed. Though we do not yet know how long Lau Basin vent communities persist, our data suggest that they may be more stable than vents found in other fast-spreading centers.

This documented stability and potential longevity of Lau vent communities could have serious implications for the

proposed mining of similar sites in the Western Pacific. Although animal communities in the EPR may be well-adapted to frequent disturbances such as eruptions and changes in vent flow patterns, our results indicate that succession progresses more slowly in Western Pacific vents, and therefore these animals may not be adapted to frequent and potentially catastrophic disturbances. Therefore, anthropogenic disturbance from deep-sea mining could have a more profound effect on these communities than previously envisioned.

Biological interactions—Succession in the Lau Basin seems to be driven primarily by changes in environmental conditions (autogenic succession), but biological interactions (allogenic succession) may also be important. Allogenic succession in animal communities has often been demonstrated in relation to vegetation change (MacMahon 1981; Kaufmann 2001). In benthic communities, allogenic succession not related to vegetation has been documented in a number of instances. For example, tube-building polychaetes facilitate the settlement of other taxa in an intertidal sandflat (Gallagher et al. 1983), the vent vestimentiferan *Tevnia jerichonana* facilitates the settlement of two other species of vestimentiferans in Eastern Pacific vents (Mullineaux et al. 2000), and Mullineaux et al. (2003) found that biological interactions strongly affect initial settlement, even in the absence of changes to the vent fluid flow regime. Furthermore, on hydrothermal vent edifices, Sarrazin et al. (1997) proposed a dynamic succession model in which at least two transitions between successional stages are driven largely by biological interactions such as biomineralization or flow modification. However, environmental conditions, particularly oxygen levels, have also been shown to be a driving force behind succession in benthic communities (Nilsson and Rosenberg 2000). Cuvelier et al. (2011) found that more subtle environmental conditions such as the orientation of edifice structures can affect faunal variations. For example, the orientation of edifice structures can affect hydrothermal activity, substrate permeability, exposure to currents, and local turbulence, which can determine the amount of colonization by different species on edifice walls.

The specific nature of biological interactions that can affect faunal abundances at stable sites in ELSC–VFR vents is not known, though it is possible that inter- or intra-species biogenic cues are used to facilitate settlement and recruitment. Margalef (1963) and MacArthur and Connell (1966) state that succession is mainly driven by environmental change brought about by the species in the communities themselves. It has been hypothesized that the symbiont-containing faunal groups in the Lau Basin can change local conditions by dispersing vent flow and consuming sulfide as has been observed with mussels in the Galapagos Spreading Center (Johnson et al. 1994).

Vestimentiferans and mussels in other vent and seep environments provide habitat for smaller organisms that colonize the shells and tubes of the dominant symbiotic fauna. Experimental studies have shown that the vent vestimentiferan *Riftia pachyptila* significantly affects the composition of the macrofaunal community (Govenar and

Fisher 2007), and the small gastropod *Bathynnerita naticoidea* responds to biological cues from the seep mussel *B. childressi* and not the environmental cues of the seep habitat (Dattagupta et al. 2007). Indeed, many organisms colonize the shells of the snails and mussels in the ELSC–VFR, and quantitative collections of these communities reveal that the associated communities differ significantly between mollusks (K. A. Zelnio unpubl.). More quantitative work will be needed to better understand how changing physico–chemical conditions and movement of the habitat-forming fauna affect the community dynamics of these smaller animals associated with them.

Implications for life histories and dispersal of Lau Basin fauna—Though we were able to document site-wide changes and test a priori hypotheses regarding succession at the ELSC–VFR, this study also generated additional hypotheses regarding the life-history characteristics and reproductive strategies of the different faunal groups. All vent fauna have some characteristics of r-selected species; however, because *Alviniconcha* spp. can sustain high levels of sulfide consumption (Henry et al. 2008) and has high tolerance for harsh environmental conditions (Podowski et al. 2010), we hypothesize that it has the fastest growth rates of the symbiont-containing faunal groups of the Lau Basin and has highly dispersed embryos. Larvae are likely numerous and small to ensure maximum dispersibility. Reynolds et al. (2010) found that female *I. nautili* brood larvae and we hypothesize that (similar to some species of polychaetes; Toonen and Pawlik 1994) this species has two different types of larvae—founders, which colonize new areas of venting; and gregarious larvae, which settle in areas already occupied by adult conspecifics. We hypothesize that *B. brevior* has the lowest growth rates and, similar to its congener *Bathymodiolus thermophilus* from the Eastern Pacific, is the most persistent of the Lau symbiont-containing fauna. Another interesting avenue of future research is the cues utilized by the different species regarding settlement of the larvae. It is probable that *Alviniconcha* spp. cues in on environmental conditions such as temperature or sulfide because individuals settle in areas where there might not be any fauna present. Snails are known to use olfactory cues to detect and move toward prey (Copeland 1918) and it is possible that larvae detect the presence of vents based on sulfide in the water, although this is likely possible only over short distances due to the rapidity with which sulfide gets oxidized in the presence of regular deep-sea water. *I. nautili* and *B. brevior* may use biogenic cues from the different species or conspecifics. There is evidence to suggest that other vent species, such as vestimentiferan tubeworms, use biogenic cues to reduce habitat selection error (Mullineaux et al. 2000); and such biogenic cues could also play a role in settlement of Lau fauna. Recently, it has been shown that larvae in a number of taxa (such as fish, cnidarians, and crabs) can use acoustic cues while settling (Heenan et al. 2008; Stanley et al. 2009; Vermeij et al. 2010). Similar to coral reefs, hydrothermal vents have a distinct soundscape (Crone et al. 2006), and it is possible that species use acoustic cues to locate vent habitats.

Importantly, even after venting has ceased, sites are unlikely to be completely devoid of animals. The substrate created by hydrothermal venting, be it lavas such as basalts and andesites or sulfide edifices, initially host hydrothermal vent communities but eventually these communities are replaced by regular hard-bottom deep-sea fauna. These fauna, including deep-sea corals and echinoderms, have much lower energy requirements than vent fauna and therefore these communities are much more stable and long-lived than the vent communities they replaced. Continued monitoring of these sites and studies of peripheral sites will contribute significantly to our understanding of these deep-sea communities.

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References

- ANTONIADOU, C., E. VOULTSIADOU, AND C. CHINTIROGLOU. 2010. Benthic colonization and succession on temperate sublittoral rocky cliffs. *J. Exp. Mar. Biol. Ecol.* **382**: 145–153, doi:10.1016/j.jembe.2009.11.004
- BEAUCHAMP, JR., R. O., J. S. BUS, J. A. POPP, C. J. BOREIKO, AND D. A. ANDJELKOVICH. 1984. A critical review of the literature on hydrogen sulfide toxicity. *Crit. Rev. Toxicol.* **13**: 25–97, doi:10.3109/10408448409029321
- BEINART, R. A., AND OTHERS. 2012. Evidence for the role of endosymbionts in regional-scale habitat partitioning by hydrothermal vent symbioses. *Proc. Natl. Acad. Sci. USA* **109**: E3241–E3250, doi:10.1073/pnas.1202690109
- BREITBURG, D. L. 1985. Development of a subtidal epibenthic community: Factors affecting species composition and the mechanisms of succession. *Oecologia* **65**: 173–184, doi:10.1007/BF00379215
- BROWN, V. K., AND A. C. GANGE. 1992. Secondary plant succession: How is it modified by insect herbivory? *Vegetatio* **101**: 3–13, doi:10.1007/BF00031910
- CHILDRESS, J. J., AND C. R. FISHER. 1992. The biology of hydrothermal vent animals: Physiology, biochemistry and autotrophic symbioses. *Ocean. Mar. Biol. Annu. Rev.* **30**: 337–441.

- CLEMENTS, F. E. 1936. Nature and structure of the climax. *J. Ecol.* **24**: 252–284, doi:10.2307/2256278
- CONNELL, J. H., AND R. O. SLATYER. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**: 1119–1144, doi:10.1086/283241
- COPELAND, M. 1918. The olfactory reactions and organs of the marine snails *Alectrion obsoleta* (Say) and *Busycon canaliculatum* (Linn.). *J. Exp. Zool.* **25**: 177–227, doi:10.1002/jez.1400250107
- COPLEY, J. T. P., P. B. K. JORGENSEN, AND R. A. SOHN. 2007. Assessment of decadal-scale ecological change at a deep Mid-Atlantic hydrothermal vent and reproductive time-series in the shrimp *Rimicaris exoculata*. *J. Mar. Biol. Assoc. U. K.* **87**: 859–867, doi:10.1017/S0025315407056512
- , P. A. TYLER, C. L. DOVER, A. SCHULTZ, P. DICKSON, S. SINGH, AND M. SULANOWSKA. 1999. Subannual temporal variation in faunal distributions at the TAG hydrothermal Mound (26° N, Mid-Atlantic Ridge). *Mar. Ecol.* **20**: 291–306, doi:10.1046/j.1439-0485.1999.2034076.x
- CORDES, E. E., S. HOURDEZ, B. L. PREDMORE, M. L. REDDING, AND C. R. FISHER. 2005. Succession of hydrocarbon seep communities associated with the long-lived foundation species *Lamellibrachia luyesi*. *Mar. Ecol. Prog. Ser.* **305**: 17–29, doi:10.3354/meps305017
- COULSON, S. J., I. D. HODKINSON, AND N. R. WEBB. 2003. Aerial dispersal of invertebrates over a high-Arctic glacier foreland: Midtre Lovénbreen, Svalbard. *Polar Biol.* **26**: 530–537, doi:10.1007/s00300-003-0516-x
- CRONE, T. J., W. S. D. WILCOCK, A. H. BARCLAY, AND J. D. PARSONS. 2006. The sound generated by Mid-Ocean Ridge black smoker hydrothermal vents. *PLoS ONE* **1**: e133, doi:10.1371/journal.pone.0000133
- CUVELIER, D., AND OTHERS. 2009. Distribution and spatial variation of hydrothermal faunal assemblages at Lucky Strike (Mid-Atlantic Ridge) revealed by high-resolution video image analysis. *Deep-Sea Res. Part I* **56**: 2026–2040, doi:10.1016/j.dsr.2009.06.006
- , AND OTHERS. 2011. Community dynamics over 14 years at the Eiffel Tower hydrothermal edifice on the Mid-Atlantic Ridge. *Limnol. Ocean.* **56**: 1624–1640, doi:10.4319/lo.2011.56.5.1624
- DAHLHOFF, E., J. OBRIEN, G. SOMERO, AND R. VETTER. 1991. Temperature effects on mitochondria from hydrothermal vent invertebrates—evidence for adaptation to elevated and variable habitat temperatures. *Physiol. Zool.* **64**: 1490–1508.
- DATTAGUPTA, S., J. MARTIN, S. LIAO, R. S. CARNEY, AND C. R. FISHER. 2007. Deep-sea hydrocarbon seep gastropod *Bathynnerita naticoidea* responds to cues from the habitat-providing mussel *Bathymodiolus childressi*. *Mar. Ecol.* **28**: 193–198, doi:10.1111/j.1439-0485.2006.00130.x
- DESBRUYÈRES, D., A.-D. ANNE-MARIE, S. OHTA, THE SCIENTIFIC PARTIES OF BIOLAU AND STARMER CRUISES. 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, doi:10.1016/0025-3227(94)90178-3
- DUDLEY, T. L., AND C. M. D'ANTONIO. 1991. The effects of substrate texture, grazing, and disturbance on macroalgal establishment in streams. *Ecology* **72**: 297–309, doi:10.2307/1938923
- EDWARDS, P. J., M. P. GILLMAN. 1987. Herbivores and plant succession, p. 295–314. *In* A. J. Gray, M. J. Crawley, and P. J. Edwards [eds.], 1987. Colonisation, succession and stability. Blackwell Scientific.
- FABRI, M. C., A. BARGAIN, P. BRIAND, A. GEBRUK, Y. FOUQUET, M. MORINEAUX, AND D. DESBRUYÈRES. 2011. The hydrothermal vent community of a new deep-sea field, Ashadze-1, 12°58'N on the Mid-Atlantic Ridge. *J. Mar. Biol. Assoc. U. K.* **91**: 01, 1–13, doi:10.1017/S0025315410000731
- FARRELL, T. M. 1989. Succession in a rocky intertidal community: The importance of disturbance size and position within a disturbed patch. *J. Exp. Mar. Biol. Ecol.* **128**: 57–73, doi:10.1016/0022-0981(89)90092-0
- . 1991. Models and mechanisms of succession: An example from a rocky intertidal community. *Ecol. Monogr.* **61**: 95–113, doi:10.2307/1943001
- FISHER, C. R., K. TAKAI, AND N. LE BRIS. 2007. Hydrothermal vent ecosystems. *Oceanography* **20**: 14–23, doi:10.5670/oceanog.2007.75
- GALLAGHER, E. D., P. A. JUMARS, AND D. D. TRUEBLOOD. 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology* **64**: 1200–1216, doi:10.2307/1937829
- GLEASON, H. A. 1927. Further views on the succession-concept. *Ecology* **8**: 299–326, doi:10.2307/1929332
- GLOVER, A. G., AND OTHERS. 2010. Temporal change in deep-sea benthic ecosystems: A review of the evidence from recent time-series studies. *Adv. Mar. Biol.* **58**: 1–95, doi:10.1016/B978-0-12-381015-1.00001-0
- GOVENAR, B., AND C. R. FISHER. 2007. Experimental evidence of habitat provision by aggregations of *Riftia pachyptila* at hydrothermal vents on the East Pacific Rise. *Mar. Ecol.* **28**: 3–14, doi:10.1111/j.1439-0485.2007.00148.x
- , M. FREEMAN, D. C. BERGQUIST, G. A. JOHNSON, AND C. R. FISHER. 2004. Composition of a one-year-old *Riftia pachyptila* community following a clearance experiment: Insight to succession patterns at deep-sea hydrothermal vents. *Biol. Bull.* **207**: 177–182, doi:10.2307/1543204
- GRASSLE, J. F. 1985. Hydrothermal vent animals: Distribution and biology. *Science* **229**: 713–717, doi:10.1126/science.229.4715.713
- HÅGVAR, S. 2010. Primary succession of springtails (Collembola) in a Norwegian glacier foreland. *Arct. Antarct. Alp. Res.* **42**: 422–429, doi:10.1657/1938-4246-42.4.422
- HEENAN, A., S. D. SIMPSON, AND V. A. BRAITHWAITE. 2008. Testing the generality of acoustic cue use at settlement in larval coral reef fish. *Proc. Intl. Coral Reef Symp., Ft. Lauderdale.* **1**: 554–558. <http://www.nova.edu/ncr/11icrs/proceedings/files/m16-13.pdf>
- HENRY, M. S., J. J. CHILDRESS, AND D. FIGUEROA. 2008. Metabolic rates and thermal tolerances of chemoautotrophic symbioses from Lau Basin hydrothermal vents and their implications for species distributions. *Deep-Sea Res. Part I* **55**: 679–695, doi:10.1016/j.dsr.2008.02.001
- HESSLER, R. R., W. M. SMITHEY, M. A. BOUDRIAS, C. H. KELLER, R. A. LUTZ, AND J. J. CHILDRESS. 1988. Temporal change in megafauna at the Rose Garden hydrothermal vent (Galapagos Rift; Eastern tropical Pacific). *Deep-Sea Res. Part I* **35**: 1681–1709.
- HIXON, M. A., AND W. N. BROSTOFF. 1996. Succession and herbivory: Effects of differential fish grazing on Hawaiian coral-reef algae. *Ecol. Monogr.* **66**: 67–90, doi:10.2307/2963481
- HODKINSON, I. D., N. R. WEBB, AND S. J. COULSON. 2002. Primary community assembly on land—the missing stages: Why are the heterotrophic organisms always there first? *J. Ecol.* **90**: 569–577, doi:10.1046/j.1365-2745.2002.00696.x
- HOLM, S. 1979. A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* **6**: 65–70.
- JANNASCH, H. W., AND M. J. MOTTL. 1985. Geomicrobiology of deep-sea hydrothermal vents. *Science* **229**: 717–725, doi:10.1126/science.229.4715.717

- JOHNSON, K. S., C. L. BEEHLER, C. M. SAKAMOTO-ARNOLD, AND J. J. CHILDRESS. 1986. In situ measurements of chemical distributions in a deep-sea hydrothermal vent field. *Science* **231**: 1139–1141, doi:10.1126/science.231.4742.1139
- , J. J. CHILDRESS, C. L. BEEHLER, AND C. M. SAKAMOTO. 1994. Biogeochemistry of hydrothermal vent mussel communities: The deep-sea analogue to the intertidal zone. *Deep-Sea Res. Part I* **41**: 993–1011, doi:10.1016/0967-0637(94)90015-9
- JOHNSTON, D. W., AND E. P. ODUM. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. *Ecology* **37**: 50–62, doi:10.2307/1929668
- KAUFMANN, R. 2001. Invertebrate succession on an alpine glacier foreland. *Ecology* **82**: 2261–2278, doi:10.1890/0012-9658(2001)082[2261:ISOAAG]2.0.CO;2
- LESSARD-PILON, S., M. D. PORTER, E. E. CORDES, I. MACDONALD, AND C. R. FISHER. 2010. Community composition and temporal change at deep Gulf of Mexico cold seeps. *Deep-Sea Res. Part II* **57**: 1891–1903, doi:10.1016/j.dsr2.2010.05.012
- LILLEY, M. D., J. A. BAROSS, AND L. I. GORDON. 1983. Reduced gases and bacteria in hydrothermal vent fluids: The Galapagos Spreading Center and 21°N East Pacific Rise, p. 411–449. *In* P. A. Rona [ed.], *Hydrothermal processes at seafloor spreading centers*. Plenum Press.
- LUTHER, G. W. I., AND OTHERS. 2000. Sulfur speciation monitored in situ with solid state gold amalgam voltammetric microelectrodes: Polysulfides as a special case in sediments, microbial mats and hydrothermal vent waters. *J. Environ. Monit.* **3**: 61–66, doi:10.1039/b006499h
- , AND OTHERS. 2008. Use of voltammetric solid-state (micro)electrodes for studying biogeochemical processes: Laboratory measurements to real time measurements with an in situ electrochemical analyzer (ISEA). *Mar. Chem.* **108**: 221–235, doi:10.1016/j.marchem.2007.03.002
- LUTZ, R. A., T. M. SHANK, R. M. HAYMON, M. D. LILLEY, K. L. VON DAMM, AND D. DESBRUYÈRES. 1994. Rapid growth at deep-sea vents. *Nature* **371**: 663–664, doi:10.1038/371663a0
- MACARTHUR, R. H., AND J. H. CONNELL. 1966. *The biology of populations*, Wiley.
- MACMAHON, J. A. 1981. Successional processes: Comparisons among biomes with special reference to probable roles of and influences on animals, p. 277–304. *In* D. C. West, H. H. Shugart, and D. B. Botkin [eds.], *Forest succession: Concepts and applications*. Springer.
- MAJER, J. D. [ED.], *Animals in primary succession: The role of fauna in reclaimed land*. Cambridge Univ. Press.
- MARCUS, J., V. TUNNICLIFFE, AND D. A. BUTTERFIELD. 2009. Post-eruption succession of macrofaunal communities at diffuse flow hydrothermal vents on Axial Volcano, Juan de Fuca Ridge, Northeast Pacific. *Deep-Sea Res. Part II* **56**: 1586–1598, doi:10.1016/j.dsr2.2009.05.004
- MARGALEF, R. 1963. On certain unifying principles in ecology. *Am. Nat.* **97**: 357–374, doi:10.1086/282286
- MATTHAEI, C. D., AND C. R. TOWNSEND. 2000. Long-term effects of local disturbance history on mobile stream invertebrates. *Oecologia* **125**: 119–126, doi:10.1007/PL00008883
- MCCOOK, L. J. 1994. Understanding ecological community succession: Causal models and theories, a review. *Plant Ecol.* **110**: 115–147, doi:10.1007/BF00033394
- MCCORMICK, P. V., AND R. J. STEVENSON. 1991. Mechanisms of benthic algal succession in lotic environments. *Ecology* **72**: 1835–1848, doi:10.2307/1940982
- MICKEL, T., AND J. CHILDRESS. 1980. Temperature and pressure responses of the Galapagos hydrothermal vent crab, *Bythograea thermydron*. *Am. Zool.* **20**: 834–834.
- , AND ———. 1982. Effects of pressure and temperature on the EKG and heart rate of the hydrothermal vent crab *Bythograea thermydron* (Brachyura). *Biol. Bull.* **162**: 70–82, doi:10.2307/1540971
- MULLINEAUX, L. S., C. R. FISHER, C. H. PETERSON, AND S. W. SCHAEFFER. 2000. Tubeworm succession at hydrothermal vents: Use of biogenic cues to reduce habitat selection error? *Oecologia* **123**: 275–284, doi:10.1007/s004420051014
- , C. H. PETERSON, F. MICHELI, AND S. W. MILLS. 2003. Successional mechanism varies along a gradient in hydrothermal fluid flux at deep-sea vents. *Ecol. Monogr.* **73**: 523–542, doi:10.1890/02-0674
- NILSSON, H. C., AND R. ROSENBERG. 2000. Succession in marine benthic habitats and fauna in response to oxygen deficiency: Analysed by sediment profile-imaging and by grab samples. *Mar. Ecol. Prog. Ser.* **197**: 139–149, doi:10.3354/meps197139
- ODUM, E. P. 1950. Bird populations of the Highlands (North Carolina) Plateau in relation to plant succession and avian invasion. *Ecology* **31**: 587–605, doi:10.2307/1931577
- . 1969. The strategy of ecosystem development. *Science* **164**: 262–270, doi:10.1126/science.164.3877.262
- PIZARRO, O., AND H. SINGH. 2003. Toward large-area mosaicking for underwater scientific applications. *Ocean. Eng. IEEE J.* **28**: 651–672, doi:10.1109/JOE.2003.819154
- PODOWSKI, E. L., S. MA, G. W. LUTHER, III, D. WARDROP, AND C. R. FISHER. 2010. Biotic and abiotic factors affecting distributions of megafauna in diffuse flow on andesite and basalt along the Eastern Lau Spreading Center, Tonga. *Mar. Ecol. Prog. Ser.* **418**: 25–45, doi:10.3354/meps08797
- , T. S. MOORE, K. A. ZELNIO, G. W. LUTHER, AND C. R. FISHER. 2009. Distribution of diffuse flow megafauna in two sites on the Eastern Lau Spreading Center, Tonga. *Deep-Sea Res. Part I* **56**: 2041–2056, doi:10.1016/j.dsr.2009.07.002
- RESH, V. H., AND OTHERS. 1988. The role of disturbance in stream. *J. North Am. Benthol. Soc.* **7**: 433–455, doi:10.2307/1467300
- REWALD, B., A. EPEL, O. SHELEFM, A. HILL, A. DEGU, A. FRIEDJUNG, AND S. RACHMILEVITCH. 2012. Hot desert environments, p. 196–218. *In* E. M. Bell [ed.], *Life at extremes: Environments, organisms and strategies for survival*. CABI.
- REYNOLDS, K. C., AND OTHERS. 2010. New molluscan larval form: Brooding and development in a hydrothermal vent gastropod, *Ifremeria nautiliei* (Provannidae). *Biol. Bull.* **219**: 7–11.
- SARRAZIN, J., V. ROBIGO, S. K. JUNIPER, AND J. R. DELANEY. 1997. Biological and geological dynamics over four years on a high-temperature sulfide structure at the Juan de Fuca Ridge hydrothermal observatory. *Mar. Ecol. Prog. Ser.* **153**: 5–24, doi:10.3354/meps153005
- SEN, A., AND OTHERS. 2013. Distribution of mega fauna on sulfide edifices on the Eastern Lau Spreading Center and Valu Fa Ridge. *Deep-Sea Res. Part I* **72**: 48–60, doi:10.1016/j.dsr.2012.11.003
- SHANK, T. M., D. J. FORNARI, K. L. VON DAMM, M. D. LILLEY, R. M. HAYMON, AND R. A. LUTZ. 1998. Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9° 50' N, East Pacific Rise). *Deep-Sea Res. Part II* **45**: 465–515, doi:10.1016/S0967-0645(97)00089-1
- SMITH, V. G. 1928. Animal communities of a deciduous forest succession. *Ecology* **9**: 479–500, doi:10.2307/1929416
- SOSA, W. P. 1984. Intertidal mosaics: Patch size, propagule availability, and spatially variable patterns of succession. *Ecology* **65**: 1918–1935, doi:10.2307/1937789
- STANLEY, J. A., C. A. RADFORD, AND A. G. JEFFS. 2009. Induction of settlement in crab megalopae by ambient underwater reef sound. *Behav. Ecol.* **21**: 113–120, doi:10.1093/beheco/arp159

- TOONEN, R. J., AND J. R. PAWLIK. 1994. Foundations of gregariousness. *Nature* **370**: 511–512, doi:10.1038/370511a0
- TRUONG, D. H., M. A. EGHBAL, W. HINDMARSH, S. H. ROTH, AND P. J. O'BRIEN. 2006. Molecular mechanisms of hydrogen sulfide toxicity. *Drug Metab. Rev.* **38**: 733–744, doi:10.1080/03602530600959607
- TSURUMI, M. 1998. The application of geographical information systems to biological studies at hydrothermal vents. *Cah. Biol. Mar.* **39**: 263–266.
- TUNNICLIFFE, V., AND K. S. JUNIPER. 1990. Dynamic character of the hydrothermal vent habitat and the nature of sulphide chimney fauna. *Prog. Ocean.* **24**: 1–13, doi:10.1016/0079-6611(90)90015-T
- VÄISÄNEN, R. A., AND O. JÄRVINEN. 1977. Quantitative structure and primary succession of bird communities in a Finnish archipelago. *Ornis Scand.* **8**: 47–60, doi:10.2307/3675987
- VAN DOVER, C. L. 2000. The ecology of deep-sea hydrothermal vents, 1st ed. Princeton Univ. Press.
- . 2011. Tighten regulations on deep-sea mining. *Nature* **470**: 31–33, doi:10.1038/470031a
- VERMEIJ, M. J., K. L. MARHAVER, C. M. HUIJBERS, I. NAGELKERKEN, AND S. D. SIMPSON. 2010. Coral larvae move toward reef sounds. *Plos One* **5**: e10660, doi:10.1371/journal.pone.0010660
- ZELNIO, K. A., E. RODRIGUEZ, AND M. DALY. 2009. Hexacorals (Anthozoa: Actiniaria, Zoanthidea) from hydrothermal vents in the south-western Pacific. *Mar. Biol. Res.* **5**: 547–571, doi:10.1080/17451000902729662

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