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# Comparative study of vent and seep macrofaunal communities in the Guaymas Basin

M. Portail<sup>1</sup>, K. Olu<sup>1</sup>, E. Escobar-Briones<sup>2</sup>, J. C. Caprais<sup>1</sup>, L. Menot<sup>1</sup>, M. Waeles<sup>3</sup>,  
P. Cruaud<sup>4</sup>, P. M. Sarradin<sup>1</sup>, A. Godfroy<sup>4</sup>, and J. Sarrazin<sup>1</sup>

<sup>1</sup>Institut Carnot Ifremer EDROME, Centre de Bretagne, REM/EEP, Laboratoire Environnement Profond, 29280 Plouzané, France

<sup>2</sup>Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, AP 70-305, Ciudad Universitaria, México

<sup>3</sup>Université de Bretagne Occidentale, IUEM, Lemar UMR CNRS 6539, 29280 Plouzané, France

<sup>4</sup>Laboratoire de Microbiologie des Environnements Extrêmes, UMR6197, IFREMER, UBO, CNRS, Technopôle Brest Iroise, 29280 Plouzané, France

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Correspondence to: M. Portail (marie.portail@ifremer.fr)

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## Abstract

Understanding the ecological processes and connectivity of chemosynthetic deep-sea ecosystems requires comparative studies. In the Guaymas Basin (Gulf of California, Mexico), the presence of seeps and vents in the absence of biogeographic barrier, comparable sedimentary settings and depths offers a unique opportunity to assess the role of ecosystem specific environmental conditions on macrofaunal communities. Six seep and four vent assemblages were studied, three of which were characterised by common major foundation taxa: vesicomid bivalves, siboglinid tubeworms and microbial mats. Macrofaunal community structure at the family level showed that density, diversity and composition patterns were primarily shaped by seep and vent common abiotic factors including methane and hydrogen sulphide concentrations. The type of substratum and the heterogeneity provided by foundation species were identified as additional structuring factors and their roles were found to vary according to fluid regimes. Surprisingly, the presence of vent environmental specificities, with higher temperature, higher metal concentrations and lower pH was not significant in explaining community patterns. Moreover, Guaymas seep and vent shared an important number of common species suggesting frequent connections between the two ecosystems. Finally, this study provides further support for the hypothesis of continuity among deep-sea seep and vent ecosystems.

## 1 Introduction

Cold-seep ecosystems are related to active and passive margins and along transform faults, whereas hydrothermal vents occur along the mid-ocean ridge systems, back-arc basins and off-axis submarine volcanoes. According to their geological contexts, deep-sea cold-seep and hydrothermal vent ecosystems involve distinct geochemical processes that give rise to fluid emissions from beneath the seafloor. At seeps, high pore-fluid pressures within sediments result in emissions of buried interstitial fluids

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mainly composed of hydrocarbons (e.g. methane) produced from the biogenic and thermogenic degradation of organic matter. As these fluids reach the upper sediment layers, methane is oxidised by microbial consortia, concomitantly with sulphate reduction by the anaerobic oxidation of methane (AOM), resulting in high hydrogen sulphide emission at the water–sediment interface (Boetius et al., 2000; Valentine, 2002; Sibuet and Olu, 1998; Kojima, 2002; Coleman and Ballard, 2001). In contrast, at vents, seawater penetrates in the ocean crust fissures and heats up until advection processes initiate the rise of hot fluids (up to 400 °C) on the seafloor. The fluid composition becomes highly complex in contact with subsurface rocks, with enriched concentrations in trace, minor and major elements, methane, hydrogen sulphide, hydrogen gas and dissolved metals (Von Damm, 1995; Jannasch and Mottl, 1985).

Although seeps and vents belong to two different geological contexts, both ecosystems are characterised by fluid emissions that present unusual properties, such as the presence of high concentrations of toxic compounds, steep physico-chemical gradients and significant temporal variation at small spatial scales (Tunnicliffe et al., 2003). Therefore, seeps and vents can be considered as extreme ecosystems for life. On the other hand, they generate energy-rich fluids that sustain high local microbial chemosynthetic production in deep-sea ecosystems, which are usually food-limited (Smith et al., 2008). There, bacteria and archaea rely mainly on the oxidation of methane and hydrogen sulphide, which are the two most common reduced compounds in vents and seeps (McCollom and Shock, 1997; Dubilier et al., 2008; Fisher, 1990). Reliance on chemosynthetic production and tolerance to environmental conditions underlie the predominant role of fluid input in both ecosystems. These chemosynthetic ecosystems therefore share many ecological homologies. They harbour macrofaunal communities that are heterogeneously distributed in a mosaic of dense assemblages defined by the presence of foundation species. These foundation species include siboglinid polychaetes (vestimentiferan tubeworms, frenulate and monoliferan pogonophorans), vesicomyid and bathymodiolid bivalves, alvinellid tube-dwelling worms, and several gastropod families, which have developed numerous strategies to adapt to their extreme

environments (toxicity) and often live in association with symbiotic bacteria (Grieshaber and Völkel, 1998; Childress and Fisher, 1992). These species, together with dense microbial mats dominated by *Beggiatoa*, thereby form various habitats that are colonised by macrofaunal communities. Across vent and seep ecosystems, these foundation species may have similar autogenic and allogenic engineering effects on associated communities (Cordes et al., 2010; Govenar, 2010). Globally, vent and seep communities share a high level of endemism, elevated macrofaunal densities and relatively low taxonomic diversity in comparison to non-chemosynthetic deep-sea ecosystems (Tunnicliffe and Fowler, 1996; Sibuet and Olu, 1998; Carney, 1994). Communities also share some families and genera presenting evolutionary connections via common ancestors, with many transitions between vent and seep habitats over geological time (Tunnicliffe et al., 1998; Tyler et al., 2002). Rapidly, the evidence of evolutionary and functional homologies highlighted potential links between the two ecosystems. This hypothesis was reinforced by the presence of seep and vent shared species and by the discovery of additional chemosynthetic stepping-stones such as large organic falls (Smith and Baco, 2003; Smith and Kukert, 1989). Moreover, macrofaunal communities at a recently discovered hybrid seep and vent ecosystem called a “hydrothermal seep”, associated with a subducting seamount on the convergent Costa Rica margin, harboured both seep and vent features, thus providing additional support for the hypothesis of continuity among reducing ecosystems (Levin et al., 2012).

Despite these numerous homologies, comparison of seeps and vents at the macrofaunal community level have revealed striking differences. Comparative studies have proposed that seeps exhibit higher diversity and lower endemism than vents (Sibuet and Olu, 1998; Turnipseed et al., 2003, 2004; Levin, 2005; Bernardino et al., 2012). Furthermore, the number of species shared on a global scale between the two ecosystems is less than 10 % of the total recorded species (e.g. Tunnicliffe et al., 2003, 1998; Sibuet and Olu, 1998). In addition, a recent review of several sedimented sites in the Pacific Ocean also points to strong dissimilarities between vent and seep macrofaunal communities even at the family level (up to 93 %) (Bernardino et al., 2012). These strong

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differences are assumed to be partly shaped by large-scale factors because seep and vent ecosystems are usually separated by long distances. Their biogeographic isolation and subsequent evolutionary divergence, as well as the closer proximity of seeps to continents (and the resulting settlement of background macrofauna) may play an important role in structuring these communities (Carney, 1994; Baker et al., 2010). Nevertheless, in the Japan Sea, a region where a total of 42 seep and vent ecosystems are found in close proximity, the similarity between seep and vent species reached only 28 % (Watanabe et al., 2010; Sibuet and Olu, 1998; Nakajima et al., 2014). In addition to large-scale factors, contrasting seep and vent environmental conditions may contribute to the strong differences among communities. Despite variation in environmental conditions in each type of ecosystem, due to the multiplicity of geological contexts and environmental settings in which seep and vent occur, vents are usually considered as more prohibitive to life than seeps. Vent sites usually exhibit greater temperature anomalies, higher metal concentrations, lower pH and oxygen concentrations as well as higher outflow rates and temporal instability than seeps (Tunnicliffe et al., 2003; Sibuet and Olu, 1998; Herzig and Hannington, 2000). Therefore, ecological processes driving community dynamics and regulating community structure may indeed differ in seeps and vents. Although the reliance on chemical energy underlies the central role of reduced chemical concentrations in both ecosystems, additional vent-specific factors may lead to distinct community structure patterns among ecosystems and thus explain, at least partly, the lower diversity at vents compared with seeps. Furthermore, these distinct environmental conditions may be responsible for the low species overlap between seeps and vents, in addition to the different physiological stress regimes that can act as “ecosystem filters”. Nevertheless, the effect of vent-specific environmental factors on the structure of macrofaunal communities are not well known due to strong correlations among physico-chemical factors (Johnson et al., 1988), preventing estimation of their respective effects (Govenar, 2010; Sarrazin et al., 1999). Overall, the key questions that remain to be addressed involve the relative influences of large

scale factors and environmental conditions on vent and seep macrofaunal community dissimilarities (Bernardino et al., 2012).

The Guaymas Basin is one of the only areas in the world that harbours both ecosystems in close proximity. Located in the central portion of the Gulf of California, Mexico, the Guaymas Basin is a young spreading centre where hydrothermal vents are found at less than 60 km from cold seeps without apparent biogeographic barrier, at comparable depths (around 2000 m) and in a similar sedimentary setting (Simoneit et al., 1990; Lonsdale et al., 1980). Therefore, this study site offers a unique opportunity to assess and compare the role of local seep and vent environmental factors on macrofaunal communities. Moreover, the presence of the same Vesicomidae bivalve species, *Archivesica gigas* (Dall, 1895), with genetic exchanges among Guaymas seep and vent suggest a current or recent connectivity between the two ecosystems (Arnaud-Haond, unpublished data).

Here, we compared the structure (abundance, diversity and composition) of Guaymas seep and vent macrofaunal assemblages in relation to their environmental conditions. The following questions were addressed: (1) what are the similarities and differences in geochemistry, microbial processes and potential engineering effects of foundation species within and between ecosystems? (2) Does the structure of seep and vent macrofaunal communities differ and which abiotic and biotic factors can best explain community structure patterns? And finally, (3) what is the level of macrofaunal overlap between the two ecosystems and how does it relate to environmental conditions? We test whether macrofaunal communities, sustained by chemical energy, show density and diversity patterns governed by reduced compound concentrations at both seep and vent sites, and whether the composition of macrofauna is ecosystem-dependent. Specifically, we test whether macrofaunal overlap is larger among diffuse, low fluid-flow sites than in more focused venting of hot fluids at vents, where vent-specific niches may exist.

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## 2 Materials and methods

### 2.1 Study area

This study focused on three areas in the Guaymas Basin located in the central portion of the Gulf of California (Fig. 1): (1) cold seeps on the Sonora margin transform faults (27°36' N, 111°29' W) at 1550 m depth, (2) a large hydrothermal field on the Southern Trough depression (27°00' N, 111°24' W) at 1900 m depth and (3) an off-axis reference site (27°25' N, 111°30' W) located at 1500 m depth (Lonsdale et al., 1980; Simoneit et al., 1990; Paull et al., 2007).

The Guaymas Basin is characterised by exceptionally high sedimentation rates due to the high biological productivity in surface waters which produce a particulate organic carbon flux of  $\sim 2400 \text{ mg C m}^{-2} \text{ d}^{-1}$  and a sedimentation rate of  $2.7 \text{ mm y}^{-1}$  (Thunell et al., 2007; Von Damm et al., 1985; Dean et al., 2004). Consequently, the Guaymas Basin is lined with a 1–2 km layer of organic-rich, diatomaceous sediments (Schrader, 1982; Calvert, 1966).

The Sonora margin transform faults are located along the eroding crest of a steep anticline (Simoneit et al., 1990; Paull et al., 2007). They are structurally similar to continental shelf pockmarks and have been named “hydrocarbon seeps” due to the emission of methane and higher hydrocarbon components. Their geochemistry is still poorly known (Simoneit et al., 1990). Extensive carbonate concretions have been reported in this area (Paull et al., 2007). Macrofaunal communities of the Sonora seep are mostly unknown and only foundation species have been described (Simoneit et al., 1990; Paull et al., 2007).

The Southern Trough spreading segment is characterised by magmatic intrusions that drive an upward hydrothermal flux through the organic-rich overlying sediments and maintain a recharging seawater circulation (Gieskes et al., 1982; Lonsdale and Becker, 1985; Fisher and Becker, 1991). Vent fluids emanate diffusely through the water–sediment interface at temperatures less than 200 °C or through mounds and chimneys rising over the seafloor where temperatures can reach up 350 °C (Von

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1974). Some specimens of *Calyptogena pacifica* (Dall, 1891) vesicomys were sampled in qualitative peripheral samples at the Ayala and Vasconcelos sites. Finally, at the Juarez site, two assemblages were sampled: (5) S\_Sib characterised by *Escarpia spicata* (Jones, 1985) and *Lamellibrachia barhami* (Webb, 1969) siboglinid tubeworms established on carbonate concretions and (6) S\_Sib\_P corresponding to the presence of reduced sediments in the immediate periphery of S\_Sib.

*Southern Trough* – a total of four vent assemblages were studied (Fig. 2). At the Mega Mat site, a microbial mat assemblage was sampled: (1) V\_Mat, characterised by the presence of white *Beggiatoa* sp. microbial mats surrounded by yellow *Beggiatoa* sp. mats. At the Morelos site, a Vesicomysidae assemblage was sampled: (2) V\_VesA characterised by *A. gigas* vesicomysid. At the Mat Mound site, a siboglinid assemblage on a 3–4 m high sulphide mound was sampled: (3) V\_Sib characterised by *Riftia pachytila* (Jones, 1981) embedded in microbial mats. Finally, at the Rebecca's Roots site, an alvinellid assemblage was sampled on the 13 m edifice: (4) V\_Alv characterised by the presence of *Paralvinella grasslei* (Desbruyères and Laubier, 1982) and *P. bactericola* (Desbruyères and Segonzac, 1997).

### 2.3 Characterisation of physico-chemical conditions

To characterise the habitats of the different assemblages, all sampling and measurements were performed in close proximity to the organisms (Table 1). Habitat temperatures were recorded using the Nautilie temperature probe. Water samples were collected in Fenwal Transfer Pack<sup>tm</sup> containers (2L, Baxter) using the PEPITO sampler implemented on the Nautilie submersible. The samples were pumped with a titanium-Tygon inlet associated with the Nautilie temperature probe. Immediately after submersible recovery, the containers were brought to a clean laboratory and filtered through 0.45 µm Millipore<sup>®</sup> HATF filters for further quantification of dissolved metals (Fe, Mn and Cu). Fe and Mn were determined using inductively coupled plasma-optical emission spectrometry (ICP-OES) (Ultima 2, Horiba Jobin Yvon, Pôle Spectrométrie Océan), whereas Cu was measured using a gold microwire electrode

(Salaün and van den Berg, 2006). pH measurements (NBS scale) were performed on board using a Metrohm glass electrode. Methane concentrations were quantified using the headspace technique (HSS 86.50, DaniInstruments) and a gas chromatograph (Perichrom 2100, Alpha MOS) equipped with a flame-ionization detector (Sarradin and Caprais, 1996).

For characterising soft-sediment habitats, we took additional temperature measurements within the sediment layer, using a 50 cm long graduated temperature sensor as well as push-core samples. The pore waters were extracted from each 0–2 cm sections along cores and analysed for methane, hydrogen sulphide, sulphate and ammonium concentrations following procedures described in (Caprais et al., 2010; Vigneron et al., 2013; Russ et al., 2013). The CALMAR benthic chamber (Caprais et al., 2010) was used to characterise the methane flux at the interface of vesicomyid assemblages.

Data on physico-chemical factors were analysed on all habitats or only on soft-sediment habitats. To compare all habitats, physico-chemical factors from water measurements on hard substratum habitats were examined against physico-chemical factors from sediment pore waters in soft sediment habitats. For both types of substrata, physico-chemical factors were separated into “interface” and “maximum” concentrations, which represented fluid input proxies. On hard substrata, the “interface” values corresponded to the measurements made close to the substratum and “maximum” values were selected from all measurements made within the three-dimensional assemblages. Similarly, soft sediment physico-chemical conditions from pore waters were summarised as interface values (0–2 cm) and maximum values along the depth of the cores (10 cm).

## 2.4 Quantification of sedimentary microbial populations using quantitative PCR

At each location, a sediment push core was collected for microbiological analyses (Table 1). After recovery on board, sediment cores were immediately transferred to a cold room (~ 8 °C) for sub-sampling. Sediment cores (0–10 cm) were sub-sampled in 2 cm

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Software (see protocol in Sarrazin et al., 1997). Each sampled area was outlined and analysed five times to estimate mean surface values. This method probably underestimates the sampled surfaces due to the omission of relief or thickness of the macrofaunal coverage, inducing a bias in density estimates but no other method is yet available to quantitatively sample the macrofauna on hard substrata in the deep sea (Gauthier et al., 2010).

### 2.5.1 Foundation species

The distribution of foundation species was used a priori to define assemblages; we therefore excluded them from the community level study. Furthermore, these species can have both allogenic (e.g. bioturbation, sulphide pumping) and autogenic (e.g. habitat provision) engineering effects on the structure of macrofaunal communities (Governar, 2010). For consistent approximation of potential engineering effects across assemblages, we used biomass (ash-free dry weight (AFDW) without tubes for siboglinids and without shells for vesicomyids and gastropods) and densities of foundation species as proxies for their biological activity and habitat provision.

### 2.5.2 Macrofaunal communities

Sediment macrofaunal samples were sliced into layers (0–1, 1–3, 3–5 and 5–10 cm). All sediment sub-samples and hard substrata samples were then sieved on a stack of four sieves of decreasing mesh sizes (1, 0.5, 0.3 and 0.25 mm). The samples were fixed in 4 % buffered formaldehyde for 24 h then preserved in 70 % alcohol. In the laboratory, only macrofauna (> 250 µm) sensu stricto (i.e. excluding meiofaunal taxa) (Hessler and Jumars, 1974; Dinét et al., 1985) were sorted, counted and identified. Identification was done to the lowest taxonomic level possible with particular attention paid to dominant taxa. Polychaete morphological identifications at the species level were not systematically reached due to the sieving process which often damages the organisms. Bivalve identifications were made in collaboration with Elena Krylova (Shirshov Institute

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of Oceanology, Russia), although a large number of juveniles could not be identified to the species level. Gastropods were exhaustively characterised in collaboration with Anders Warén (Swedish Museum of Natural History, Sweden). Because it was not always possible to determine to the species level, comparisons of the macrofaunal community were done at the family level, except for some taxa with low contributions to macrofaunal densities, such as Aplacophora, Sipuncula, Scaphopoda, Nemertina, Cumacea, Tanaidacea and Amphipoda.

## 2.6 Data analyses

At the assemblage scale, considering the low level of replication within some assemblages ( $n$  varied between 1 and 4, Table 5) and differences in sampling strategies between soft and hard substrata, data analyses mainly relied upon descriptive statistics. Rarefaction curves and Hurlbert's ES( $n$ ) diversity index were computed using the Biodiversity R package (Kindt and Coe, 2005) and the functions in Gauthier et al. (2010) on pooled abundances per assemblage. The ES( $n$ ) measure of diversity was used because this index is the most suitable for non-standardised sample sizes (Soetaert and Heip, 1990). Spearman rank correlations were carried on physico-chemical variables, foundation species descriptors and associated macrofaunal community density and ES( $n$ ) diversity. Two levels of analysis were applied: one considering all assemblages sampled (hard and soft) and a subset focusing on soft-substratum assemblages, thereby allowing the addition of supplementary physico-chemical variables and the abundance of microbes potentially involved in AOM. Parametric regression models were tested for ES( $n$ ) and macrofaunal density in relation to physico-chemical conditions to compare our data with previous studies.

Community composition analyses were based on Hellinger-transformed family densities to conserve Hellinger, rather than Euclidian, distances in PCA. The Hellinger distance gives a lower weight to dominant taxa and avoids considering double absence as an indicator of similarity between samples (Legendre and Gallagher, 2001). Canonical redundancy analyses (RDA), considering all assemblages, included hard and soft

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substrata qualitative variable as well as normalised physico-chemical variables and foundation species descriptors. On soft substrata, a co-inertia analysis (CIA) was carried out first on normalised physico-chemical factors and the abundance of microbial groups potentially involved in AOM. The CIA summarise most of the co-variance between physico-chemical variables and microbial processes across sedimentary habitats into a limited number of independent variables (the first  $x$  axes of the CIA). These new variables, which can be considered to depict the biogeochemical environment of each habitat, were then used as explanatory variables in a RDA, together with the proxies of the engineering effects of foundation species. For all RDA analyses, forward selection with a threshold  $p$  value of 0.1 was used to sort the significant explanatory variables. The significance of CIA and RDA were tested with permutation tests (Legendre and Legendre, 2012).

At the ecosystem level and among the three vesicomid assemblages for which comparisons were possible, mean comparisons were done using the non-parametric Kruskal–Wallis test, followed by a LSD rank test for pairwise comparisons (Steel and Torrie, 1997). The Sorensen index was used to estimate and compare the beta diversity of the seep and vent ecosystems based on presence/absence data. Sorensen dissimilarity was decomposed according to turnover and nestedness, which result from two antithetic processes, namely species replacement and species loss (Baselga, 2010).

All analyses were performed in the R environment (R Development Core Team, 2014). Multivariate analyses were carried out using `rdaTest` function and `vegan` (Oksanen et al., 2015), `ade4` (Dray and Dufour, 2007) and `betapart` (Baselga and Orme, 2012) packages.

## 3 Results

### 3.1 Environmental description

#### 3.1.1 Physico-chemical conditions

*All assemblages* – temperature and methane concentrations were the only two physico-chemical variables that were measured across all assemblages, including hard and soft substrata (Table 2a). Interface and maximum values were always correlated ( $R$ : 0.9,  $p < 0.001$ ). Thus, only maximal values are presented herein.

No temperature anomalies in comparison to ambient bottom seawater (which is at  $2.9^\circ\text{C}$  in the Guaymas Basin) were found in seep sites, neither on hard substrata, nor within the sediments. At vents, all sites showed temperature anomalies with maximum temperature of  $\sim 7^\circ\text{C}$  at V\_VesA,  $\sim 20^\circ\text{C}$  at V\_Alv,  $\sim 30^\circ\text{C}$  at V\_Sib and  $\sim 56^\circ\text{C}$  at V\_Mat. Thus, temperature anomalies were specific to vents.

Maximum methane concentrations at the Guaymas reference site (G\_Ref) were low ( $\sim 1\ \mu\text{M}$ ). At seeps, maximum methane concentrations ranged from  $\sim 1$  to  $800\ \mu\text{M}$ , separating assemblages into two habitat groups, one showing low concentrations ( $\sim 1$  to  $30\ \mu\text{M}$ ), i.e. S\_VesA, S\_Sib\_P, S\_VesP and S\_Sib, and the other, high concentrations ( $\sim 700$  to  $800\ \mu\text{M}$ ), represented by S\_Gast and S\_Mat. At vents, maximum methane concentrations ranged from  $\sim 50$  to  $\sim 900\ \mu\text{M}$  with low concentrations ( $\sim 50\ \mu\text{M}$ ) found at V\_VesA and high concentrations ( $\sim 300$  to  $900\ \mu\text{M}$ ) at V\_Sib, V\_Alv and the highest concentrations found at V\_Mat. While fluid fluxes were not measured systematically, methane flux was null at G\_Ref,  $\sim 2\ \text{mmol m}^{-2}\ \text{d}^{-1}$  at S\_VesA and S\_VesP and  $\sim 9\ \text{mmol m}^{-2}\ \text{d}^{-1}$  at V\_VesA (Table 2b).

Methane concentrations were positively correlated with temperature anomalies ( $R$ : 0.5,  $p < 0.05$ ): vent sites often showed high methane concentrations whereas seep sites generally had low methane concentrations. Furthermore, after exclusion of seep sites, vent methane concentrations and temperatures were highly correlated ( $R$ : 0.9,  $p < 0.05$ ).

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*Soft sediment assemblages* – in soft-sediment assemblages, hydrogen sulphide, sulphates and ammonium concentrations were also compared (Table 2a). Again, interface and maximum values were always correlated ( $R > 0.7$ ,  $p < 0.05$ ). Thus, only maximal values are presented herein.

As expected, hydrogen sulphide concentrations were positively correlated with methane concentrations ( $R > 0.8$ ,  $p < 0.01$ ) while sulphate concentrations were negatively correlated with both hydrogen sulphide and methane concentrations ( $R > 0.7$ ,  $p < 0.05$ ). Hydrogen sulphide was not detected at the reference site G\_ref. At seeps, maximum hydrogen sulphide concentrations ranged from undetected to  $\sim 30\,000\ \mu\text{M}$ , with no detection throughout the 10 cm sediment core at S\_VesP, S\_VesA and S\_Sib\_P. High concentrations were found at S\_Gast ( $\sim 15\,000\ \mu\text{M}$ ) and S\_Mat ( $\sim 30\,000\ \mu\text{M}$ ). At vents, maximum hydrogen sulphide concentrations in the two soft-sediment sites ranged from  $\sim 1700$  to  $\sim 9000\ \mu\text{M}$ , with the lowest concentration found at V\_VesA and the highest at V\_Mat.

Maximum ammonium concentrations were positively correlated to temperature, being higher at vents than seeps ( $R > 0.8$ ,  $p < 0.05$ ). Maximum ammonium concentrations at seeps ranged from  $\sim 26$  to  $\sim 56\ \mu\text{M}$ , close to the G\_Ref reference site values ( $13\ \mu\text{M}$ ). Vent maximum ammonium concentrations were much higher at V\_VesA ( $384\ \mu\text{M}$ ) and V\_Mat ( $1800\ \mu\text{M}$ ).

Overall, seep and vent assemblages were classified into two habitat groups according to the concentrations of reduced compounds, regardless of the ecosystem, with higher fluid inputs at two seep sites (S\_Gast, S\_Mat) and three vent sites (V\_Sib, V\_Alv and V\_Mat), whereas four seep sites (S\_Sib, S\_SibP, S\_VesA and S\_VesP) and one vent (V\_VesA) site showed lower fluid inputs, closer to those found at the Guaymas reference site (G\_Ref). Despite some variations, seep and vent microbial mat (S\_Mat, V\_Mat) and vesicomid (S\_VesA, S\_VesP, V\_VesA) habitats belonged to the same respective groups, whereas seep and vent siboglinid (S\_Sib and V\_Sib) habitats strongly differed. The seep siboglinid site was characterised by lower fluid input than the vent siboglinid site. Although methane and hydrogen sulphide showed comparable concen-

5 tration ranges among seep and vent ecosystems, temperature anomalies and ammonium concentrations were specific to vents. In addition, other compounds not available for all assemblages suggest further differences between seeps and vents. For example, the patterns of pH and Mn concentrations discriminated vents from seeps rather than habitats across ecosystems (Table 2b). Mean Mn concentrations were significantly higher at vents than at seeps (Kruskal–Wallis test,  $p < 0.05$ ) while mean pH was significantly lower at vents (Kruskal–Wallis test,  $p < 0.05$ ). These differences reflect the specific input of hydrothermal fluid in those assemblages.

### 3.1.2 Microbial populations with respect to the physico-chemical conditions

10 Microbial populations potentially involved in AOM processes co-varied with physico-chemical conditions in the CIA performed on soft-sediment assemblages (Fig. 3, Table 3). The relationships were statistically significant ( $p = 0.01$ ). According to the first axis, which contributed to 85 % of the variance, high methane and hydrogen sulphide concentrations and low sulphate concentrations were associated with high abundances of ANMEs 1 and 2 at one end, corresponding to S\_Mat, V\_Mat and S\_Gast assemblages. The second axis, which accounted for 15 % of the variance, was driven by temperature anomalies and high  $\text{NH}_4$  concentrations at V\_Mat, where a higher frequency of ANME1 and a lower frequency of ANME2 and DSS were found compared with S\_Mat and S\_Gast. The first CIA axis thus summarised the variance due to chemosynthetic processes and can be considered a proxy for fluid input across vent and seep ecosystems, whereas the second axis of the CIA summarised environmental conditions that are specific to vents.

### 3.1.3 Foundation species descriptors

25 *Seep assemblages* – *L. barhami* and *E. spicata* siboglinids at S\_Sib were characterised by long thin tubes. They reached a density of  $720 \text{ ind m}^{-2}$  and a biomass of  $457 \text{ g m}^{-2}$  (AFDW) (Table 4). *A. gigas* vesicomid at S\_VesA and *P. soyoae* species at S\_VesP



V\_Mat) and vesicomylid assemblages (S\_VesA, S\_VesA, V\_VesA), whereas those of siboglinid assemblages (S\_Sib, V\_Sib) differed strongly, being higher at vents. Among the three vesicomylid assemblages, density differences were close to being significant ( $p = 0.07$ ). Significant differences were found with higher densities at the seep *A. gigas* assemblage (S\_VesA) compared with the vent *A. gigas* (V\_VesA) and seep *P. soyoae* (S\_VesP) assemblages ( $p < 0.05$ ), with the latter assemblages showing comparable densities.

Macrofaunal densities did not show any significant correlation with physico-chemical factors. However, log-transformed densities showed that along the range of maximal methane concentrations, densities appeared to be first enhanced at seep and vent vesicomylid assemblages (S\_VesP, S\_VesA, V\_VesA) together with seep siboglinids (S\_Sib) and their periphery (S\_Sib\_P) compared to the reference site (G\_Ref) while highest methane concentrations at seep and vent microbial mats (S\_Mat, V\_Mat) were related to minimum densities of all chemosynthetic assemblages (Fig. 4). In between, high density fluctuations were found among vent alvinellid (V\_Alv) and vent siboglinid (V\_Sib) assemblages, despite relatively comparable maximal methane concentrations. A similar pattern was found between seep gastropod assemblage (S\_Gast) compared with seep and vent microbial mats (S\_Mat, V\_Mat). In addition, a polynomial relationship between macrofaunal community density and foundation species density was found with S\_Gast and V\_Sib assemblages harbouring higher densities of both foundation species and associated communities than the other assemblages ( $R = 0.8$ ,  $p < 0.05$ ).

### 3.2.2 Alpha diversity patterns

As seen on rarefaction curves, the diversity was relatively well characterised depending on the assemblage. Four curves, corresponding to G\_ref, V\_VesA, V\_Mat and S\_Mat assemblages, did not reach an asymptote (Fig. 5), indicating an insufficient sampling effort. The sampling effort at V\_Mat and G\_ref (2 LBC and 4 SBS respectively) was

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and overestimated at three assemblages (S\_Gast, V\_Sib and V\_Alv). There was no visible discrimination between seep and vent ecosystems.

### 3.2.3 Community composition patterns

At the reference site (G\_Ref), Polychaeta dominated the community (90.2%) with Bivalvia, Aplacophora and Cnidaria representing less than 5% of the community (Fig. 7). In terms of families, G\_Ref was dominated by Cirratulidae (29%) followed by Nereididae and Paraonidae (each 12%), Ampharetidae (10%) and Spionidae (7%), the other taxa accounting for less than 5% of the abundance.

At seeps, macrofaunal composition was dominated by Polychaeta (from 57.3 to 99.8%) with the exception of S\_VesP where Bivalvia dominated (53.9%) (Fig. 7). In all assemblages, Gastropoda represented less than 5% of the specimens, except at S\_Sib and S\_VesP, where they reached higher relative abundances (38.2 and 16.9%, respectively). Ophiuroidea represented > 5% of the community composition at S\_VesP (7.1%) and S\_VesA (6%). Aplacophora formed less than 5% of the community in all assemblages except for S\_VesA, where it reached 7.2%. Malacostraca, Cnidaria, Sipunculida, Scaphopoda and Nemertina never exceeded 5% of relative abundance. Macrofaunal composition at the family level discriminated S\_Mat and S\_Gast from all of the other assemblages due to their relatively high proportion of Ampharetidae that respectively represented 32 and 69% of the abundance. In addition, S\_Mat, S\_Gast and S\_VesA shared dominance of Dorvilleidae (39, 31 and 40% respectively). Other assemblages can be distinguished by the dominance of specific families: S\_VesP had the highest frequency of Nuculanidae bivalves (52%) and Provannidae gastropods (8%), S\_Sib showed a high frequency of Lepetodrilidae (26%), Polynoidae (20%) and Serpulidae (18%) and S\_Sib\_P had a relatively high frequency of Cirratulidae (19%), Lumbrineridae (11%), Cossuridae (10%), Paraonidae (9%) and Thysaridae (6%).

At vents, similar to what was observed at seeps, Polychaeta dominated the macrofaunal composition in all assemblages (from 56.7 to 99.9%) (Fig. 7). Bivalvia, Gastropoda and Malacostraca abundances were found at frequencies higher than 5% only

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at V\_VesA where they formed respectively 19.4, 15 and 7.2 % of the community. Aplousobranchia represented less than 5 % of the abundance. At the family level, Dorvilleidae dominated at all sites, with maximum relative abundance found at V\_Sib (91 %) followed by V\_Mat (75 %), V\_Alv (59 %) and V\_VesA (40 %) (Fig. 7). Ampharetidae were found in all assemblages, with highest abundances in V\_Mat (16 %) followed by V\_Sib (9 %), V\_VesA (8 %) and V\_Alv (3 %). V\_Alv was characterised by high abundance of Polynoidae (37 %). At V\_Mat, some Nereididae, Thyasiridae, Provannidae and Hesionidae were found but they collectively accounted for only 10 % of the abundance. V\_VesA had a higher frequency of Provannidae (9 %) and of taxa such as Bathyspinulidae (16 %), Amphipoda (7 %), Neomphaloidae (6 %) and Cirratulidae (4 %).

Macrofaunal community composition at the family level was analysed using a between-groups PCA, a particular case of RDA that tests and maximises the variance between assemblages. Together, the three first axes accounted for 51 % of the total variance in community composition (Fig. 8). The intra-assemblage heterogeneity was relatively high, but lower than the inter-assemblage variability, with the exception of S\_VesA and V\_VesA in which there was a slight overlap (Fig. 8). The first axis of the PCA accounted for 27 % of the variability in community composition, mostly separating the G\_ref and S\_Sib\_P assemblages dominated by Cirratulidae, Paraonidae and Spirochaetidae polychaetes from the V\_Sib, V\_Mat, V\_Alv, S\_Gast and S\_Mat assemblages, characterised by higher frequencies of Dorvilleidae and Ampharetidae polychaetes. Intermediate compositions were found at S\_Sib\_P, S\_VesP, S\_VesA and V\_VesA. The second axis accounted for 14 % of the variance in macrofaunal community composition. It was mainly influenced by the dominance of Bathyspinulidae at S\_VesP. The third axis accounted for 10 % of the variance, differentiating in particular the S\_Sib assemblage, characterised by the presence of Polynoidae, Lepetodrilidae, Neolepetopsidae, Serpulidae and Nereididae.

Overall, although the heterogeneity between macrofaunal communities appeared higher at seeps than at vents, there was no discrimination between vent and seep assemblages (Fig. 8). Community compositions across seep and vent common micro-

bial mats (S\_Mat, V\_Mat) and vesicomylid (S\_VesP, S\_VesA, V\_VesA) assemblages were closely related, whereas differed according to the ecosystem they belonged to among siboglinid assemblages (S\_Sib, V\_Sib). Of the three vesicomylid assemblages, those dominated by *A. gigas* at seeps and vents (S\_VesA, V\_VesA) were more similar than those dominated by *P. soyoae* species in seeps (S\_VesP).

*Relationships with site characteristics* – the forward selection test showed that the variation of macrofaunal community composition among assemblages was significantly influenced by maximum methane concentrations and the type of substratum ( $p < 0.01$ ), whereas temperature anomalies and the biomass and density of foundation species were not significant. The first two components of the canonical redundancy analysis (RDA) accounted for respectively 27% ( $p = 0.01$ ) and 13% ( $p = 0.08$ ) of the variability in macrofaunal composition (adjusted  $R^2$ , 0.25) (Fig. 9). The first axis was mostly driven by maximum methane concentrations. The high methane concentrations at the S\_Gast, V\_Sib, V\_Mat, V\_Alv and S\_Mat sites were mainly associated with the dominance of dorvilleids and ampharetids and to a lesser extent to polynoids. The low methane concentrations at all other sites were linked to higher abundances of cirratulids, bathyspinulids, paranoids, lumbrinerids, aplacophorans, ophiurids, hesionids and neolepetopsids. Nevertheless, in this latter group, S\_VesA and V\_VesA compositions had more affinities with assemblages characterised by high methane concentrations. The second RDA axis was driven by the type of substratum (hard/soft) but also by higher methane concentrations in V\_Mat, S\_Mat and S\_Gast sites. On one end, hard substrata mainly contributed to S\_Sib and V\_Alv macrofaunal composition, with the presence of polynoids at V\_Alv coupled to that of lepetodrilids, serpulids and neolepetopsids at S\_Sib. On the other end, the higher methane concentrations in V\_Mat, S\_Mat and S\_Gast mainly accounted for the higher dominance of ampharetids whereas soft substrata appeared to explain the abundance of hesionids and bathyspinulids.

Focusing on soft sediment assemblages, the forward selection test showed that macrofaunal community composition was significantly influenced by the first axis of

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the CIA and the biomass of foundation species, which were the best explanatory variables ( $p$  values of 0.01 and 0.07, respectively). The relationship with the first axis of the CIA, which we interpreted as a proxy for fluid input across ecosystems, was highly significant, whereas the relationship with the second axis of the CIA, which we interpreted as being vent-specific, was not. The first two components of the RDA accounted for respectively 31 % ( $p = 0.03$ ) and 20 % ( $p = 0.06$ ) of the variability in macrofaunal composition (adjusted  $R^2 = 0.31$ ) (Fig. 10). According to the first axis, higher fluid inputs at seep and vent microbial mats and gastropod assemblages (S\_Mat, V\_Mat, S\_Gast) contributed to the high dominance of ampharetids and dorvilleids. At the other end, all other assemblages were characterised by a higher proportion of taxa from the Cirratulidae and Bathyspinulidae families. In this latter group, the seep and vent *A. gigas* assemblages (S\_VesA, V\_VesA) were found to have more affinities with assemblages of high fluid input than the other assemblages. The second axis was mainly driven by the biomass of foundation species, discriminating S\_VesP from the other assemblages with high frequencies of nuculanid bivalves, ophiurids, and gastropods compared with lower frequencies dominance of several polychaete families. This pattern may be also related to differences in the engineering effects of *P. soyoae* at S\_VesP, compared to *A. gigas*, at S\_VesA and V\_VesA.

### 3.2.4 Similarity in community composition between vent and seep ecosystems

At the family level, gamma diversity of macrofaunal communities that are associated to foundation species reached 56 families at the seep ecosystem, 22 families at the vent ecosystem and 15 at the reference site (G\_ref). All the families found at the reference site were also found at seep and eight of them were shared with vents. As the diversity at the reference site was estimated on only one assemblage, diversity comparison to seep and vent ones was not estimated. The Sorensen dissimilarity between seep and vent macrofaunal composition was estimated at 42 % and corresponds only to nestedness (species loss), whereas the dissimilarity linked to turnover (species replacement)

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was nil. Indeed, all the 22 families found at vent were also found at seep ecosystem while seep had 28 additional families.

26 species belonging to 18 seep and vent common families were identified (Table 6). Of these, the vast majority (22 species) were found in both ecosystems, whereas only two species of gastropods were specific to seep ecosystem (*Eulimella lomana* and *Paralepetopsis* sp.) and two were restricted to vent one (the polynoid *Branchiplicatus cupreus* and the gastropod *Pyropelta musiaca*).

## 4 Discussion

Previous comparative studies have highlighted strong differences between seep and vent macrofaunal communities (Bernardino et al., 2012; Tunnicliffe et al., 2003, 1998; Sibuet and Olu, 1998; Turnipseed et al., 2003, 2004; Watanabe et al., 2010; Nakajima et al., 2014). However, to date, large-scale ecological factors and biogeographic barriers have limited any direct comparisons of the impact of seep- and vent-specific environmental conditions. Guaymas seeps and vents have comparable sedimentary settings and depths and no biogeographic barriers, offering an ideal case study for a better understanding of chemosynthetic community density, diversity and composition patterns in regard to local environmental conditions. Although methane and hydrogen sulphide appear to be potential common structuring factors across seep and vent ecosystems, ecosystem specific fluid properties may further shape community patterns. In addition, other environmental factors such as the type of substratum and the role of foundation species as engineers add a potential complexity within communities (Govenar, 2010; Cordes et al., 2010). In our study, the comparison of seep and vent common assemblages may address the issue of the specific role of fluid input and composition on macrofaunal communities.

## 4.1 Similarities and differences in site biogeochemistry

*Substratum* – seven sampled assemblages were associated with soft sediment (at seeps: vesicomyid, microbial mat and gastropod assemblages as well as an assemblage at the periphery of a siboglinid assemblage; at vents: vesicomyid and microbial mat assemblages). Only three assemblages were associated with hard substrata (seep siboglinid assemblage, vent siboglinid and alvinellid assemblages). Of these latter hard-substratum assemblages, the nature of the hard substrata differed in the two ecosystems. At seeps, the origin of authigenic carbonates colonised by siboglinids has been attributed to AOM microbial consortiums that, through the production of DIC and the increase of pore water alkalinity, facilitate the precipitation of authigenic carbonate minerals (Paull et al., 2007). At vents, the hydrothermal fluid percolating through the sediments retains enough metals and sulphides to produce hot fluids that form large sulphide edifices, such as the Rebecca's Roost, on top of which the alvinellid assemblages were found, or smaller sulphide mounds such as Mat Mound where siboglinids have settled (Jørgensen et al., 1990).

*Vent and seep physico-chemical conditions* – in sediment-covered vent fields, fluid properties are modified when the fluid passes through the sediment layer. Therefore, fluid emissions at the water–substratum interface may strongly differ from the original end-member fluids and potentially lead to reduced seep and vent environmental discrepancies as shown elsewhere in terms of temperature and geochemistry (Sahling et al., 2005; Tunnicliffe et al., 2003; LaBonte et al., 2007; Von Damm et al., 1985).

Within our study, the high methane and hydrogen sulphide concentration ranges were similar in seep and vent ecosystems. As fluid fluxes were not measured within each assemblage, concentrations of these reduced compounds at the water–substratum interface and among sites were used as fluid input proxies. The Guaymas chemosynthetic habitats can be thus divided in two groups, regardless of the ecosystems: those with low fluid inputs (seep and vent vesicomyid assemblages, seep siboglinid assemblages and seep siboglinid periphery assemblages) and those with

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high fluid inputs (seep and vent microbial mat, seep gastropod, vent siboglinid and vent alvinellid assemblages). In addition, two of the three seep and vent common assemblages (vesicomyid and microbial mat assemblages) showed relatively comparable fluid inputs. Indeed, habitats at microbial mat assemblages are usually characterized by strong fluid inputs whereas vesicomyid habitats are related to lower fluid inputs (Levin, 2005). The third common assemblage did not exhibit the same pattern with vent siboglinid habitat related to strongly higher fluid inputs than seep one. Indeed, siboglinids at seeps and vents occupy different ecological niches along a gradient of fluid flow. The seep *L. barhami* and *E. spicata* siboglinids pump hydrogen sulphide through their roots deep in the sediment in low-flow settings (Julian et al., 1999) while the vent taxon *R. pachypila* captures the chemical elements through its gills, in stronger fluid flow (Arp and Childress, 1983).

Although the Guaymas seep and vent habitats shared comparable ranges of methane and hydrogen sulphide concentrations, vent assemblages showed temperature anomalies, which are correlated to fluid inputs, ranging from 6.5 °C in the vesicomyid assemblage to 55.5 °C in the microbial mat assemblage. Vent habitats were also characterised by higher ammonium concentrations, lower pH and higher manganese concentrations than seeps, reflecting the end-member concentration of the vent fluids (Von Damm et al., 1985). Vent enrichment in ammonium is related to the thermocatalytic percolation of sedimentary organic matter by hydrothermal fluids, a process that produces methane and petroleum-like aliphatic and aromatic hydrocarbons (Bazylinski et al., 1988; Von Damm et al., 1985; Pearson et al., 2005; Simoneit et al., 1992).

Vent-specific factors in regards of temperature, metals, pH and petroleum-like hydrocarbons may limit fauna, but not much is known about them. Although metal concentrations in Guaymas vent fluids are known to be lower than typical basalt-hosted systems, presumably due to the high alkalinity and high pH of the fluids that reduce metal solubility (Von Damm et al., 1985), heavy metals may be potentially toxic in minute quantities (Decho and Luoma, 1996). In addition, a comparative study of the Guaymas and

9°50' N vents in the East Pacific Rise (EPR) showed that concentrations in metals were lower in vent fluid but higher in organism tissues at Guaymas (Von Damm, 2000; Von Damm et al., 1985). This suggests that heavy metal bioaccumulation is independent of the total metal concentrations, but depend on metal bioavailability (Ruelas-Inzunza et al., 2003; Demina et al., 2009).

*AOM-related microbial populations* – AOM has been shown to represent a major microbial process not only at the Sonora margin cold seeps (Vigneron et al., 2013, 2014), but also in sedimented vents and in methane-rich hydrothermal sediments of the Guaymas Basin (Teske et al., 2002; Dhillon et al., 2003, 2005; Holler et al., 2011; Biddle et al., 2012). In our study, the composition of microbial communities potentially involved in AOM processes co-varied with physico-chemical conditions among soft-sediment assemblages. Variations were mainly related to higher ANME archaeal abundance at both seep and vent high fluid-input habitats. Nevertheless, compositions of ANME clades are distinct among these assemblages: ANME1 dominated at vent microbial mat assemblage whereas seep microbial mats and gastropod assemblages showed co-dominance of ANME1 and 2. Indeed, previous studies have suggested that ANME1 are associated with more stable anoxic environments and higher temperatures than ANME2 (Rossel et al., 2011; Biddle et al., 2012; Vigneron et al., 2013; Holler et al., 2011; Nauhaus et al., 2005).

*Heterogeneity of foundation species* – in addition to the type of substratum and biogeochemical conditions, foundation species may contribute to add heterogeneity within and between ecosystems through both allogenic and autogenic engineering (Govenar, 2010; Cordes et al., 2010). The tubes of siboglinid worms and the shells of bivalves can provide substratum and increase habitat complexity, promoting settlement or survivorship of associated species (Govenar, 2010). Vesicomysids that move vertically and laterally and, to a lesser extent, gastropods that can reach exceptionally high densities, may rework sediments thus increasing oxygen penetration depth and indirectly promoting sulphide production (Wallmann et al., 1997; Fischer et al., 2012). In seep habitats, siboglinid tubeworms can also stimulate sulphide production through bio-irrigation and

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the release of sulphate deep in the sediments (Cordes et al., 2005; Dattagupta et al., 2008). Foundation species can also foster access to highly productive habitats by providing colonisation surfaces for microbial mats and contributing to the segregation of organic matter (Levesque et al., 2005; Sarrazin et al., 2002). The level of heterogeneity provided by foundation species and the processes involved are however difficult to assess. In our study, three assemblages were characterised by the presence of common major taxa (siboglinids, vesicomids and microbial mats), one assemblage (*Hyalogyrina* gastropods) was only present at seeps and another (*Paralvinella* alvinellids) was only present at vents. Among siboglinid assemblages, densities were two times higher and biomass was 14 times higher for *R. pachyptila* at vents than *E. spicata* and *L. barhami* at seeps, suggesting potentially stronger engineering influence of *Riftia* bushes, particularly regarding habitat provision and complexity. Between seep *A. gigas*, seep *P. soyoae* and vent *A. gigas* vesicomid assemblages, vesicomid densities and biomasses were comparable due to high variability between samples of the same assemblage. However, visual observations of the *P. soyoae* assemblage suggest the presence of denser clusters in comparison with *A. gigas* clusters in seep and vent assemblages. Furthermore, the highest biomass was observed in the *P. soyoae* species, which also have larger sizes. In addition, the behaviour and biological traits of the two species differ. *P. soyoae* dominates at the Ayala site where individuals seemed restricted to the water–sediment interface in relatively compact sediments compared to *A. gigas* at the Vasconcelos and Morelos sites, where it lives buried in soft and fine sediments (pers. obs.). Moreover, numerous trace paths were observed around *A. gigas* assemblages, indicating high motility for this species. A similar pattern was observed between two vesicomid species in the Sea of Okhotsk (Krylova, 2014): the more mobile *Archivesica ochotica* (a closely related species to *A. gigas*) was found in relatively small aggregations in soft-sediment sites with higher sulphide levels, whereas, in contrast, *P. soyoae* lived in dense clusters, on more solidified sediment and at sites with apparently lower fluid fluxes (Krylova, 2014). *A. gigas* may thus have stronger allogenic

effects (i.e. bioturbation) while *P. soyoae*, due to its larger size and lower motility, may have stronger authigenic effects (i.e. habitat provision).

Overall, our results showed that the Guaymas seep and vent environmental conditions are characterised by comparable concentration ranges of reduced compounds (methane, hydrogen sulphide), but that they can also be differentiated in terms of type of hard substratum and vent fluid proprieties (temperature, magnesium, pH). These seep and vent physico-chemical homologies and specificities influenced microbial populations linked to AOM processes in the soft-sediment assemblages. Moreover, heterogeneity associated with the foundation species identity may further differentiate the two ecosystems with only one foundation species shared, *A. gigas vesicomid*.

Seep and vent assemblages characterized by common major taxa, siboglinids, vesicomids and microbial mats are characterized by more or less comparable environmental conditions. Strong environmental differences are found among seep and vent siboglinid assemblages with the vent one characterised by higher fluid input, a potentially stronger engineering role of foundation species and vent-specificities depicted by temperature reaching 30 °C. In contrast, among seep and vent vesicomid assemblages, relatively comparable low fluid inputs were found. In addition, despite potential variations according to the species, seep and vent vesicomids are suspected to have relatively similar engineering roles. Specific environmental conditions at the vent vesicomid assemblage were depicted by temperature of 6.5 °C and the presence of oily sediment (pers. obs.) together with slightly higher fluid flow than found at the two seep sites. Finally, seep and vent microbial mat habitats had also relatively comparable fluid-input settings, but herein related to high fluid inputs. Vent-specific environmental conditions at the microbial mat assemblage were depicted by high temperatures reaching up to 55.5 °C. Thus, in order to reinforce patterns observed among all assemblages, only comparison of vesicomid and microbial mat assemblages across ecosystems can be used to attempt to specifically assess the role of vent environmental conditions on macrofaunal communities.

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## 4.2 Community patterns and structuring factors

Bernardino et al. (2012) proposed a conceptual framework of factors shaping the biodiversity, density and biomass of macrofaunal communities within reducing ecosystems, adapted from the Pearson and Rosenberg, (1978) model. The model predicts that, within each ecosystem, density increases along a gradient of increasing fluid flow due to organic enrichment up to a threshold where fluid toxicity overwhelms the benefit of organic enrichment, thus leading to reduced densities. In parallel, the model describes a pattern of diversity as a unimodal function of fluid flow, peaking at intermediate fluid flow intensities. Low fluid intensity allows colonisation by a mix of background and chemosynthetic endemic macrofauna, whereas increasing fluid flow intensity leads to the selection of tolerant macrofauna. Likewise, many studies report that macrofaunal communities are primarily shaped by fluid flow gradients at seeps (Sibuet and Olu-Le Roy, 2003; Bergquist et al., 2003, 2005; Sahling et al., 2002; Levin et al., 2003; Decker et al., 2012; Thurber et al., 2010; Levin and Dayton, 2009; Ritt et al., 2010, 2012; Robinson et al., 2004; Olu et al., 1996) and vents (Levin et al., 2009; Matabos et al., 2008; Bates et al., 2005; Mills et al., 2007; Cuvelier et al., 2009a, b; Tunnicliffe, 1991; Sarrazin et al., 1997, 1999; Desbruyères et al., 2001; MacDonald et al., 2003; Govenar et al., 2005). Nevertheless, to date, no conceptual framework including compound concentrations consistent across the seep and vent ecosystems has been proposed.

### 4.2.1 Density and diversity patterns

Our first working hypothesis was that seep and vent macrofaunal communities exhibit density and diversity patterns that are similarly governed by methane and hydrogen sulphide fluid inputs, regardless of the ecosystem.

In the Guaymas Basin, the majority of seep and vent assemblages had higher densities than the reference site, attesting to positive, productive effect of chemosynthesis and/or to lower anoxic conditions. Indeed, despite high sedimentation within the Guaymas Basin, at 1500 m depth, organic matter may be refractory. In addition, Guaymas

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bottom waters are poorly oxygenated,  $\sim 30 \mu\text{M}$ , leading to the production of anoxic sediments (Campbell and Gieskes, 1984), whereas chemosynthetic assemblages can be found on hard substrata and foundation species may provide habitat oxygenation. Within both ecosystems, fluid inputs, depicted by methane concentrations, appear to account for a large part of the variability in faunal density. Densities at relatively low fluid-input sites were enhanced in comparison with the background sediment and the highest densities were related to two of the high fluid-input habitats (vent siboglinid assemblage, seep gastropod assemblage). Seep and vent microbial mat assemblages, which showed the highest fluid inputs, were characterised by reduced density. Interestingly, within both ecosystems, high variation in density was found among relatively comparable high fluid-input habitats. At vents, macrofaunal communities within siboglinid assemblages were denser than in the alvinellid assemblage. Similarly, at seeps, the associated community in the gastropod assemblage had higher densities than in the microbial mats. These differences may result from distinct fluid flow and/or engineering roles of foundation species among assemblages. Comparison across ecosystems of assemblages characterised by relatively comparable fluid inputs and engineering role of foundation species (microbial mat assemblages, vesicomid assemblages) did not lead to any conclusions on vent-specific effects on density.

Alpha diversity showed a more straightforward relationship to fluid input through a highly significant logarithmic correlation. Diversity appeared to be maximal in the background sediment and decreased with increasing fluid input highlighting enhanced selection of tolerant taxa along a gradient of fluid intensity. There were no significant diversity differences between the seep and vent ecosystems and comparisons of vesicomid and microbial mat assemblages across ecosystems did not confirm any effect of vent-specific conditions on diversity.

Overall, density and diversity patterns observed within each ecosystem were relatively consistent with the conceptual model proposed in Bernardino et al. (2012). Our results suggest that diversity and density patterns are shaped along a similar gradient of reduced compound concentrations, without any vent-specific effects.

## 4.2.2 Community composition patterns

Our second working hypothesis was that variation in macrofaunal composition between vents and seeps is ecosystem-dependent: more specifically, we predicted that macrofaunal overlap is larger among diffuse, low fluid-flow sites, whereas the more focused emission of hot fluids at vents creates niches that are vent-specific.

Surprisingly, the overall macrofaunal composition patterns did not differentiate seep from vent ecosystems. Substantial overlap was found among seep and vent assemblages characterised by low fluid inputs. These assemblages were colonised by similar families, including some that are endemic or extremely common in chemosynthetic ecosystems (e.g. Neolepetopsidae, Provannidae, Lepetodrilidae and Polynoidae), along with other families that are typical deep-sea sediments (e.g. Cirratulidae, Paraonidae and Spionidae) (Menot et al., 2010). Contrary to our hypothesis, high fluid-input assemblages were similar at seeps and vents. In both ecosystems, these assemblages were characterised by the presence of Ampharetidae and Dorvilleidae polychaetes, known as highly specialised taxa. Indeed, to cope with sulphide and/or thermal stress, ampharetid polychaetes live in vertical tubes from which they deploy their gills over and above the substrata as an adaptation to harsh environmental conditions (Treude et al., 2009). Dorvilleids are known to be sulphide-tolerant and often colonise heavily polluted areas (Fauchald and Jumars, 1979); they are usually found at seeps in the most sulphide-rich environments (Levin, 2005).

Comparison across ecosystems of assemblages characterised by relatively comparable fluid inputs and engineering role of foundation species (microbial mat assemblages, vesicomid assemblages) did not indicate any vent-specific effect.

In addition to fluid input, the type of substratum and the engineering influence of foundation species significantly contributed to variations in community composition within and between ecosystems. The abundance of gastropods (Lepetodrilidae, Neolepetopsidae), Polynoidae, Serpulidae and Nereididae in the siboglinid seep assemblage was significantly linked to the presence of a hard substratum. At vents, however, the com-

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position of macrofauna in the siboglinid microhabitat, and to a lesser extent in the alvinellid microhabitat, was not attributed to the presence of a hard substratum. With the exception of polynoids, the composition of these last communities resembles that found in high fluid-flow soft-substratum assemblages. The presence of a thick microbial mat at the base of *R. pachyptila* tube worms and of mucus secretions in alvinellid assemblages may have fostered colonisation by soft-substratum taxa. In addition, high fluid fluxes and temperature in the siboglinid and alvinellid vent assemblages may have restricted faunal colonisation, while relatively low fluid fluxes at siboglinid seeps may have favoured the establishment of less tolerant taxa. Furthermore, stronger engineering effect of tube worms at seeps than vents, despite their lower densities and biomass as well as compared to the alvinellids engineering role may be involved. Clearly, there is a strong interplay between fluid flow input, substratum and engineering effects in the structuring of macrofaunal communities at seeps and vents, with the influence of the latter two factors here decreasing as fluid input increases. Interestingly, lepetodrilid limpets found in the seep siboglinid assemblage are known to mainly occur at vents and the lepetodrilid *L. guaymensis* was first sampled and described from tube worms and rocks of the Guaymas Southern Through vent site (McLean, 1988). In addition, lepetodrilid limpets have also been found in *L. barhami* bushes at the Jaco Scar hydrothermal seep as were serpulids (Levin et al., 2012). In our study, the presence of these two taxa on *L. barhami* and *E. spicata* tubes and their absence in *R. pachyptila* bushes may result from the particular setting of the sampled *R. pachyptila* assemblage as suggested by the particularly thick microbial mat at the base of the tube worms, together with temperatures reaching ca. 30 °C, suggesting their immersion in sulphide-rich and hot fluid flow. Indeed, *R. pachyptila* within the Guaymas Basin has been previously found at lower fluid flow as suggested by the lower temperature measured (14 °C) (Robidart et al., 2011).

The estimation of the respective role of fluid flow and taxa engineering on the structure of macrobenthic assemblages is often a challenge within both seep and vent ecosystems because the distribution of foundation species is strongly correlated with

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fluid flow (Cordes et al., 2009; Sahling et al., 2002; Roy et al., 2007). In our study, the presence of two distinct vesicomyid-dominated assemblages (*A. gigas* and *P. soyoae*) characterised by similar fluid inputs among the seep ecosystem offered an opportunity to assess their respective roles in their associated communities. Considering their behavioural and biological traits, we expected *A. gigas* to have stronger allogenic effects (i.e. bioturbation) and *P. soyoae* to have stronger authigenic effects (i.e. habitat provision). Indeed, significant structuring effect was found related to the *P. soyoae* in comparison to the *A. gigas* species. We hypothesize that oxygenation of sediments by *A. gigas* species may explain the colonisation by the denser, species-rich endofauna dominated by polychaetes we observed whereas lower bioturbation activity in the *P. soyoae* assemblage may have limited the establishment of dense and diverse communities and reduced endofaunal taxa at the expense of epifaunal Bathyspinulidae bivalve *Nuculana* sp. Thus, these results suggest a non-negligible engineering role of foundation species on the structure of associated macrofaunal communities at the Guaymas seeps, in low fluid-flow settings. Furthermore, macrofaunal community structure variation between the two seep vesicomyid assemblages exceeded those between the seep and vent *A. gigas* assemblages. The engineering effect within seeps may thus overwhelm the effect of vent-specific factors. In addition, diversity and density differences among seep and vent *A. gigas* assemblages cannot be specifically associated with vent-specific factors (temperature, petroleum) as their environmental distinctions are also related to relatively higher fluid inputs and flows at the vent one.

Overall, Guaymas vent and seep macrofaunal communities were mainly structured by the fluid input regardless of the ecosystem. In addition, heterogeneity due to type of substratum and the foundation species appeared to vary according to abiotic conditions with an increased influence with decreasing fluid input. Comparisons of common assemblages characterised by relatively similar fluid inputs across ecosystems suggest that vent-specific conditions are not the dominant structuring factors among vesicomyid assemblages and that they did not affect the structure of macrofaunal communities in microbial mat assemblages.

### 4.3 The vent and seep connectivity

In the Guaymas Basin, comparison of macrofaunal community composition associated to foundation species did not discriminate seep and vent ecosystems due to the dominance of common families. Gamma diversity differences nevertheless still emerged between seep and vent ecosystems. In total, 56 families were found at seeps and 22 at vents, leading to a relatively high dissimilarity (42 %) between the two ecosystems. However, this value remains lower than that reported from Pacific seep and vents (93 %; Bernardino et al., 2012). Moreover, dissimilarity was characterised by nestedness rather than by species turnover because vent families represented a sub-sample of those found at seeps (i.e. all vent families were found at seeps). The higher richness found at seeps may be due to the higher sampling effort and thus, to a better characterisation of seep diversity, especially because rare species can reach up to 50 % of the communities in chemosynthetic environments (Baker et al., 2010). This effect of rare species is supported by the fact that 30 species from the 34 families exclusive to the seeps were found in low relative densities (< 5 %). Furthermore, the number of sampled sites was higher at seeps (6) than at vents (4) and high species turnover among sites is frequent at seeps (Cordes et al., 2009). A higher number of low fluid-flow assemblages were sampled at seeps (four compared with just one at vents), these being characterised by higher taxonomic richness with the presence of background taxa. In contrast, a higher number of high fluid-flow assemblages were sampled at vents (three compared with two at seeps), harbouring conditions that may prevent colonisation by certain taxa. In addition, the substratum and biogenic heterogeneity due to foundation species may have helped to enhance the beta-diversity in low fluid-flow assemblages. Overall, we suggest that the greater gamma diversity at seep ecosystem is due to the presence of a greater variety of foundation species in association with the higher environmental heterogeneity found in low fluid-input habitats at seep than vent. However, we cannot exclude the possibility of seep and vent “ecosystem filtering”, which may influence the distribution of the rare macrofaunal families, with harsher conditions at

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vents. Furthermore, comparison of seep and vent communities at the family level may affect the assessment of community structure patterns (Gauthier et al., 2010). Shallow water studies have shown that in terms of macrofauna taxonomic richness, the family and species levels are strongly correlated (e.g. (Jameson et al., 1995; Olsgard et al., 2003). Similar conclusions have also been drawn for the study of taxonomic richness in deep-sea chemosynthetic communities (Doerries and Van Dover, 2003). However, Pearson and Rosenberg (1978) suggest that increasing environmental changes are manifest at decreasing taxonomic resolutions and thus suggest that some information may still be lost in a lower range of environmental changes.

Despite these limitations, species distribution across seep and vent families of macrofaunal communities suggests a sustained exchange between chemosynthesis-based ecosystems of the Guaymas Basin (Table 6). Of the 26 species identified within 18 families common to seeps and vents, only two species were specific to seeps (*Paralepetopsis* sp., *E. lomana*) and two to vents (*P. musaica*, *B. cupreus*). These differences may even be lower because *E. lomana*, despite its absence in our vent samples, has already been collected at the Guaymas Basin vent sites (Warén and Bouchet, 1993) and *P. musaica* has been reported from eastern Pacific seep sites (Jalisco Block seeps, off Mexico: (Sasaki et al., 2010). Thus, our study suggests relatively weak “ecosystem filtering” between Guaymas seeps and vents.

In addition, the analysis of the distribution of foundation species revealed that the differences among macrofaunal communities found at the ecosystem level within our study may in fact be minimal. Of the four seep-specific foundation species (*P. soyoae*, *E. spicata*, *L. barhami* and *Hyalogyrina* sp.), two (*P. soyoae* and *E. spicata*) have already been recorded at Guaymas vents (Table 6). In addition, seep-related siboglinids have been found on authigenic carbonate crusts at an off-axis magma intrusion site within the Guaymas Northern Trough segment (Lizarralde et al., 2011) and other species found at Guaymas seeps, but not found at the vents, have already been found in other vent ecosystems: *L. barhami* has been reported in East Pacific sedimented vent areas at Middle Valley (Black et al., 1997) and *Hyalogyrina* gastropods have been

found at the periphery of microbial mats at numerous vents around the world (Sasaki et al., 2010). The absence of these assemblages within our vent study may be due to the lack of sampling at the vent periphery. In addition, although *C. pacifica* were occasionally sampled at seeps in our study, identified by both morphology (E. Krylova, personal communication, 2015) and COI sequencing (Arnaud-Haond, personal communication, 2015), no *C. pacifica* specimens were detected in the hydrothermal vent area, though some specimens of the species complex *C. pacifica/C. lepta* have been reported at Guaymas vents (Grassle et al., 1985; Simoneit et al., 1990). Although three vent foundation species, *R. pachyptila*, *P. grasslei* and *P. bactericola*, are vent-endemic, they did not appear in our study to exert an important ecosystem engineering effect on community composition, mainly due to the influence of high fluid inputs.

Overall, Guaymas seep and vent species compositions suggest that, with the exception of a few species, including the foundation species that are vent-endemic, a large part of macrofaunal communities can colonise variable ecosystems and cope with environmental variation. Therefore, our study supports strong connectivity among reducing ecosystems in the absence of biogeographic barrier. In addition, our results contribute 20 additional species to the list of species common to seeps and vents in the world's oceans (Table 6).

Finally, we suggest that the differences between seep and vent species compositions generally observed at large spatial scales may mainly reflect biogeographic barriers and heterogeneity due to foundation species identity and type of substratum. Accordingly, the ability of macrofaunal communities to adapt to seep and vent environmental specificities seems higher than previously suggested. Nevertheless, the sedimentary context of the Guaymas Basin in comparison to other settings may reduce seep and vent fluid discrepancies, allowing greater connectivity among ecosystems. Thus, more comparative studies along the seep and vent environmental continuum are needed to confirm the faunal commonality of reducing ecosystems communities.

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Macrofaunal patterns in terms of density, alpha diversity and taxonomic composition at the family level did not differentiate the two ecosystems studied here despite the presence of vent-specific environmental conditions. Structuring factors were found to be shared between the two ecosystems, including methane and hydrogen sulphide concentrations, the type of substratum and the heterogeneity due to foundation species, whereas vent-specific conditions (temperature, pH, manganese concentrations or even observed petroleum) had no significant effect on associated macrofauna. A high proportion of identified species were common to seeps and vents, highlighting the ability of macrofauna to colonise various environmental conditions. At the ecosystem scale, differences in gamma diversity with a higher overall diversity at seeps mainly reflected the presence of additional rare families. We suggest that this difference is related to the higher intrusion of background macrofauna and to the establishment of more complex and diverse communities in low-flow assemblages, which were variable at Guaymas seeps. However, our study may have overestimated these differences due to the presence of additional low-flow assemblages at Guaymas vent that have been reported, but were missing from our study.

A more functional approach is currently underway to analyse the ecological processes that occur within these communities. An assessment of the food resources, ecological niches, biotic interactions and trophic adaptations within and between Guaymas vent and seep ecosystems will pave the way to a better understanding of these chemosynthetic communities.

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**Table 1.** Location of the different assemblages sampled in the Guaymas Basin and sampling details. REFERENCE: (G\_ref), SEEPS: *P. soyoeae* Vesicomiyidae (S\_VesP), *A. gigas* Vesicomiyidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), Siboglinidae (S\_Sib), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomiyidae (V\_VesA), Microbial mat (V\_Mat), Alvinellidae (V\_Alv) and Siboglinidae (V\_Sib). Blade corers sample a surface of 180 cm<sup>2</sup> for the small blade cores (SBC) and 360 cm<sup>2</sup> for the large cores (LBC) whereas tube corer (TC) samples a surface of 26 cm<sup>2</sup>. GS = ground surface sampled.

	Latitude	Longitude	Depth (m)	Substrata	Physico-chemical characterisation	Faunal sampling
<b>Reference assemblage</b>						
G_ref	N 27 25.483	W 111 30.076	1850	Soft	2 TC 5 PEPITO 2 CALMAR	Macrofauna: 4 SBC Microbiota: 1 TC
<b>Seep assemblages</b>						
S_VesP	N 27 35.365	W 111 28.395	1561	Soft	1 TC 7 PEPITO 2 CALMAR	Macrofauna: 3 LBC Microbiota: 1 TC
S_VesA	N 27 35.587	W 111 28.963	1576	Soft	1 TC 3 PEPITO 2 CALMAR	Macrofauna: 3 LBC Microbiota: 1 TC
S_Mat	N 27 35.580	W 111 28.986	1576	Soft	2 TC 12 PEPITO	Macrofauna: 3 LBC Microbiota: 1 TC
S_Gast	N 27 35.583	W 111 28.982	1576	Soft	2 TC	Macrofauna: 1 SBC
S_Sib	N 27 35.274	W 111 28.406	1562	Hard	6 PEPITO	Suction sampler + submersible grab GS: 694 cm <sup>2</sup>
S_Sib_P	N 27 35.273	W 111 28.407	1562	Soft	1 TC	Macrofauna: 4 SBC Microbiota: 1 TC
<b>Vent assemblages</b>						
V_VesA	N 27 00.547	W 111 24.424	2007	Soft	2 TC 8 PEPITO 2 CALMAR	Macrofauna: 3 LBC Microbiota: 1 TC
V_Mat	N 27 00.445	W 111 24.530	2012	Soft	1 TC	Macrofauna: 2 LBC Microbiota: 1 TC
V_Alv	N 27 00.664	W 111 24.412	1995	Hard	2 PEPITO	Suction sampler GS: 720 cm <sup>2</sup>
V_Sib	N 27 00.386	W 111 24.576	2004	Hard	5 PEPITO	Suction sampler + submersible grab GS: 1134 cm <sup>2</sup>

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**Table 2a.** Temperature and methane concentrations measured on all assemblages (pore-water measurements within soft sediment and water measurements above hard substratum) and hydrogen sulphide, ammonium and sulphate pore-water concentrations within soft sediment assemblages. Physico-chemical factors are summarised as substratum–water interface values and maximum values measured among assemblages. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomyidae (S\_VesP), *A. gigas* Vesicomyidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), Siboglinidae (S\_Sib), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomyidae (V\_VesA), Microbial mat (V\_Mat), Alvinellidae (V\_Alv) and Siboglinidae (V\_Sib). Highest values are highlighted in bold.

	T <sub>int</sub> °C	T <sub>max</sub> °C	[CH <sub>4</sub> ] <sub>int</sub> μM	[CH <sub>4</sub> ] <sub>max</sub> μM	[H <sub>2</sub> S] <sub>int</sub> μM	[H <sub>2</sub> S] <sub>max</sub> μM	[NH <sub>4</sub> ] <sub>int</sub> μM	[NH <sub>4</sub> ] <sub>max</sub> μM	[SO <sub>4</sub> <sup>2-</sup> ] <sub>int</sub> mM	[SO <sub>4</sub> <sup>2-</sup> ] <sub>min</sub> mM
<b>Soft substrata</b>										
G_ref	2.9	2.9	0.4	0.7	0.0	0.0	11.5	12.8	27.1	<b>27.0</b>
S_VesP	2.9	2.9	0.6	13.0	0.0	0.0	13.4	47.5	26.8	26.8
S_VesA	2.9	2.9	0.4	0.7	0.0	0.0	33.0	33.0	27.0	26.5
S_Mat	2.9	2.9	<b>787</b>	803	<b>22 700</b>	<b>31 300</b>	33.8	55.9	11.7	7.1
S_Gast	2.9	2.9	192	680	2470	15600	5.4	25.6	14.8	7.2
S_Sib_P	2.9	2.9	0.6	4.6	0.0	0.0	12.4	29.8	<b>27.3</b>	26.5
V_VesA	3.1	6.5	2.1	45.7	0.0	1700	32.6	384	27.2	24.7
V_Mat	3.2	<b>55.5</b>	220	<b>890</b>	2890	9000	<b>1260</b>	<b>1800</b>	21.3	15.0
<b>Hard substrata</b>										
S_Sib	2.9	2.9	18.2	30.1	–	–	–	–	–	–
V_Alv	8.1	20.0	371	382	–	–	–	–	–	–
V_Sib	<b>22.7</b>	29.7	182	275	–	–	–	–	–	–

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**Table 2b.** Supplementary physico-chemical factors measured on some assemblages: pH, methane flux ( $F(\text{CH}_4)$ ), Total dissolved Iron (TdFe), Total dissolved Manganese (TdMn) and Total dissolved Copper (TdCu). Due to sampling limitations, these factors were not available for all assemblages. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomymidae (S\_VesP), *A. gigas* Vesicomymidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), Siboglinidae (S\_Sib), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomymidae (V\_VesA), Microbial mat (V\_Mat), Alvinellidae (V\_Alv) and Siboglinidae (V\_Sib). Standard deviations are given in parentheses and the highest values per factor are shown in bold.

	pH	$F(\text{CH}_4)$ ( $\text{mol m}^{-2} \text{d}^{-1}$ )	TdFe ( $\mu\text{M}$ )	TdMn ( $\mu\text{M}$ )	TdCu (nM)
<b>Reference assemblage</b>					
G_ref	7.5 (0.06)	−0.1 (0.3)	NA	NA	NA
<b>Seep assemblages</b>					
S_VesP	7.6 (0.12)	2.3(0.6)	0.09 (0.03)	0.02	12.5 (5.2)
S_VesA	7.5 (0.04)	1.8(0.2)	0.08 (0.08)	0.04 (0.006)	9.2 (5.1)
S_Mat	<b>7.7</b> (0.10)	NA	0.12 (0.19)	0.06 (0.07)	8.0 (5.6)
S_Sib	7.6 (0.04)	NA	0.14 (0.11)	0.16 (0.005)	9.4 (7.8)
Mean	7.6 (0.10)	–	0.10 (0.10)	0.07 (0.07)	9.6 (5.8)
<b>Vent assemblages</b>					
V_VesA	7.4 (0.05)	<b>8.5</b> (0.7)	0.06 (0.03)	0.06 (0.04)	<b>21.6</b> (28.1)
V_Mat	NA	NA	NA	NA	NA
V_Alv	6.9 (0.13)	NA	<b>0.16</b> (0.002)	0.46 (0.10)	11.5 (6.4)
V_Sib	7.0 (0.13)	NA	0.15 (0.06)	<b>1.41</b> (0.50)	2.5 (0.9)
Mean	7.2 (0.26)	–	0.10 (0.06)	0.40 (0.60)	15.7 (23.1)

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**Table 3.** Quantitative PCR results on six *Archaea* and *Bacteria* phyla potentially involved in the anaerobic oxidation of methane (AOM): ANME1, ANME2, ANME3, DSS, DBB and SRB2. Results are cumulated across the 0–10 cm sediment layer and expressed in 16S rRNA copy number per gram of sediment. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomidae (V\_VesA) and Microbial mat (V\_Mat). The highest values for each group of AOM micro-organisms are shown in bold.

	ANME1	ANME2	ANME3	DSS	DBB	SRB2
<b>Reference assemblage</b>						
G_ref	8.16E+04	1.40E+06	2.74E+06	1.10E+08	4.08E+06	5.42E+05
<b>Seep assemblages</b>						
S_VesP	3.84E+07	6.94E+07	2.32E+05	1.60E+08	4.88E+06	7.78E+06
S_VesA	1.28E+08	1.47E+08	3.42E+06	2.40E+08	4.44E+06	1.35E+06
S_Mat	7.84E+08	7.56E+08	<b>1.45E+08</b>	<b>4.72E+08</b>	4.00E+07	1.97E+07
S_Gast	<b>1.12E+09</b>	<b>1.47E+09</b>	3.38E+07	3.78E+08	<b>5.28E+07</b>	1.15E+07
S_Sib_P	5.10E+07	2.62E+08	1.65E+07	2.18E+08	3.62E+06	2.16E+06
<b>Vent assemblages</b>						
V_VesA	2.34E+05	5.28E+05	2.42E+06	1.44E+08	5.80E+06	8.60E+05
V_Mat	1.09E+09	1.17E+08	1.33E+06	7.08E+07	6.36E+06	<b>8.12E+07</b>

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**Table 4.** Characteristics of foundation species (size, density and biomass) in the Guaymas Basin. SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Gastropoda (S\_Gast), Siboglinidae (S\_Sib) and VENTS: *A. gigas* Vesicomidae (V\_VesA), Alvinellidae (V\_Alv) and Siboglinidae (V\_Sib). Standard deviations are given in parentheses and highest values are shown in bold.

Species	Length (L), Diameter (D), (mm)	Density (ind m <sup>-2</sup> )	Biomass (g m <sup>-2</sup> )
<b>Seep assemblages</b>			
S_Sib <i>Escarpia spicata/Lamellibrachia barhami</i>	L: 368 (116)/D: 6 (3)	721	457
S_VesA <i>Archivesica gigas</i>	L: 75.0 (8.9)	102 (42)	262 (119)
S_VesP <i>Phreagena soyoae</i>	L: 87.1 (27.8)	74.1 (69.9)	405 (358)
S_Gast <i>Hyalogorina</i> sp.	D: 2.0 (0.3)	<b>10 170</b>	2.4
<b>Vent assemblages</b>			
V_Sib <i>Riftia pachyptila</i>	L: <b>431</b> (133)/D: 19.9 (9)	1280	<b>6630</b>
V_VesA <i>Archivesica gigas</i>	L: 57.0 (20.6)	55.6 (48.1)	81.3 (107)
V_Alv <i>Paralvinella grasslei/Paralvinella bactericola</i>	L: 24.2 (14.4)/D: 2.2 (1.0)	1070	31.2

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**Table 5.** Macrofaunal community composition (expressed in terms of density:  $\text{ind m}^{-2}$ ) in the Guaymas Basin assemblages at the family level, including total densities ( $\text{ind m}^{-2}$ ) and  $ES_{41}$  diversity. Standard deviations are given in parentheses. The highest values observed for each assemblage are highlighted in bold. Reference: (G\_ref), SEEPS: *P. soyoae* Vesicomylidae (S\_VesP), *A. gigas* Vesicomylidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), Siboglinidae (S\_Sib), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomylidae (V\_VesA), Microbial mat (V\_Mat), Alvinellidae (V\_Alv) and Siboglinidae (V\_Sib).

	G_ref				S_VesP			S_VesA			S_Mat		
	1	2	3	4	1	2	3	1	2	3	1	2	3
<b>Bivalvia</b>													
Bathyspinulidae	0	0	0	0	<b>1778</b>	<b>361</b>	83	1417	1583	972	333	28	111
Cuspidariidae	0	0	0	0	0	0	0	28	0	0	0	0	0
Mytilidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Solemyidae	0	0	0	0	28	56	0	0	28	0	0	0	0
Thyasiridae	0	56	0	0	0	0	0	0	0	56	0	0	0
<b>Gastropoda</b>													
Aplustridae	0	0	0	0	0	0	0	0	0	28	0	0	0
Cataegidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyalogyrinidae	0	0	0	0	28	0	0	0	0	28	0	0	0
Lepetodrilidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Neolepetopsidae	0	0	0	0	56	83	111	28	56	0	0	0	0
Neomphaloidae	0	0	0	0	0	0	0	0	56	0	0	0	0
Provannidae	0	0	0	0	167	167	0	56	0	0	0	0	0
Pyramidellidae	0	0	0	0	0	83	28	28	0	0	0	0	0
Pyropeltidae	0	0	0	0	0	0	0	0	28	0	0	0	0
<b>Polychata</b>													
Acoetidae	0	0	0	0	0	0	0	0	28	0	0	0	0
Ampharetidae	0	167	0	56	0	0	0	556	1806	56	<b>806</b>	0	28
Amphinomidae	0	0	0	0	0	0	0	28	0	0	0	0	0
Archinomidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Capitellidae	0	0	56	0	56	0	0	0	83	0	0	0	0
Cirratulidae	<b>167</b>	<b>278</b>	56	<b>167</b>	28	28	<b>167</b>	444	194	1056	28	0	0
Cossuridae	0	0	0	0	0	0	0	250	28	444	0	0	0
Dorvilleidae	0	0	0	0	28	28	<b>167</b>	<b>6472</b>	<b>3889</b>	<b>2750</b>	361	<b>472</b>	<b>194</b>

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**Table 5.** Continued.

	S_Gast 1	S_Sib 1	S_Sib_P		3	4	V_VesA			V_Mat		V_Alv 1	V_Sib 1
			1	2			1	2	3	1	2		
<b>Bivalvia</b>													
Bathyspinulidae	0	144	556	167	333	111	167	222	<b>417</b>	0	0	0	0
Cuspidariidae	0	0	0	0	56	56	0	0	0	0	0	0	0
Mytilidae	0	86	0	0	0	0	0	0	0	0	0	0	71
Solemyidae	0	0	0	0	0	0	0	28	0	0	0	0	0
Thyasiridae	55.6	58	56	389	222	389	28	111	0	28	0	0	0
<b>Gastropoda</b>													
Aplustridae	0	58	0	0	0	0	28	0	0	0	0	0	0
Cataegidae	0	130	0	0	0	0	0	0	0	0	0	0	18
Hyalogyrinidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepetodrilidae	0	<b>2104</b>	0	0	0	0	0	0	0	0	0	14	0
Neolepetopsidae	0	735	0	0	0	0	0	0	0	0	0	0	0
Neomphaloidae	0	0	0	0	0	0	0	250	28	0	0	0	0
Provannidae	0	43	0	0	0	0	417	28	0	0	28	0	0
Pyramidellidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyropeltidae	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>Polychata</b>													
Acoetidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Ampharetidae	<b>17 222</b>	0	0	0	0	0	167	28	194	139	83	86	8269
Amphinomidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Archinomidae	0	87	0	0	0	0	0	0	0	0	0	0	0
Capitellidae	0	0	111	0	0	0	0	0	0	0	0	0	0
Cirratulidae	0	29	<b>944</b>	167	<b>944</b>	<b>1444</b>	111	56	28	0	0	0	0
Cossuridae	0	0	611	222	722	389	0	0	0	0	0	0	0
Dorvilleidae	7611	231	556	<b>1944</b>	556	167	<b>500</b>	<b>1389</b>	111	<b>444</b>	<b>611</b>	<b>1543</b>	<b>85 946</b>

Table 5. Continued.

	G_ref				S_VesP			S_VesA			S_Mat		
	1	2	3	4	1	2	3	1	2	3	1	2	3
Flabelligeridae	0	0	0	0	0	0	0	28	28	0	0	0	0
Glyceridae	0	0	0	56	28	0	0	28	0	0	0	0	0
Goniadidae	0	0	0	0	0	0	0	28	0	0	0	0	0
Hesionidae	0	0	0	56	0	0	0	1278	583	167	111	0	28
Lacydonidae	0	0	0	0	0	0	0	278	0	56	0	0	0
Lumbrineridae	0	0	0	0	0	0	28	361	139	250	0	0	0
Maldanidae	0	0	0	0	28	0	56	56	56	28	0	0	0
Nautiniellidae	0	0	0	0	0	56	0	0	28	0	0	0	0
Nephtyidae	0	0	0	0	0	0	0	0	0	111	0	0	0
Nereididae	56	222	0	0	0	0	0	83	194	28	0	0	0
Opheliidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Paraonidae	167	56	56	0	0	0	0	167	0	222	0	0	0
Pholoidae	0	56	0	0	0	0	0	28	0	28	0	0	0
Phyllodocidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Pilargidae	0	0	111	0	0	0	0	56	0	83	0	0	0
Polynoidae	0	0	0	0	0	0	0	28	0	83	28	0	0
Serpulidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigalionidae	0	56	0	56	0	0	0	0	0	28	0	0	0
Sphaerodoridae	0	0	0	0	0	0	0	139	83	83	0	0	0
Spionidae	56	111	0	0	0	0	0	28	56	83	0	0	0
Sternaspidae	0	0	0	0	0	0	0	28	0	28	0	0	0
Syllidae	0	0	0	0	0	0	0	0	0	0	0	27	0
Terrebellidae	0	0	0	0	139	0	0	56	28	0	0	0	0
Trichobranchidae	0	0	0	0	0	0	0	0	0	28	0	0	0
<b>Others</b>													
Actinaria	0	56	0	0	0	56	0	83	0	0	0	0	0
Amphipoda	0	0	0	0	0	0	0	0	56	28	0	0	0
Aplacophora	0	0	56	56	0	0	56	1250	917	222	28	0	0
Cnidaria	0	0	0	0	0	0	0	28	28	0	0	0	0
Cumacea	0	0	0	0	0	0	0	0	0	0	56	0	0
Nemertina	0	0	0	0	0	0	0	194	389	56	0	0	0
Ophiuridae	0	0	0	0	83	194	28	306	861	833	0	0	0
Scaphopoda	0	0	0	0	0	0	0	0	0	0	0	0	0
Sipuncula	0	0	0	0	0	0	0	167	28	0	0	0	0
Tanaidacea	0	0	0	0	0	0	0	0	28	0	0	0	0
Total density	446	1058	335	447	2447	1112	724	14 005	11 281	7835	1751	527	361
Mean density		569 (328)			1426 (903)			11 037 (3090)			880 (762)		
ES <sub>41</sub>		14			11.1			12.2			6.4		



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**Table 6.** Presence/absence of seep and vent species in the Guaymas Basin (\*: not found within our study but previously recorded in Guaymas) and species records from other studies in the Costa Rica “hydrothermal seep” (CRHS) and more generally, at cold seeps (CS), vents (HV) or organic falls (OF) around the world.

	Guaymas	Guaymas	CRHS	CS	HV	OF	References
	Seep	Vent					
<b>Foundation species</b>							
<b>Vesicomyidae</b>							
<i>Phreagena soyaoe</i>	x	x*		x	x	x	Baco et al. (1999), Audzijonyte et al. (2012)
<i>Archivesica gigas</i>	x	x	x	x	x	x	Krylova and Sahling (2010), Audzijonyte et al. (2012), Smith et al. (2014), Levin et al. (2012a)
<i>Calyptogena pacifica</i>	x			x	x	x	Huber (2010), Audzijonyte et al. (2012), Smith et al. (2014)
<b>Alvinellidae</b>							
<i>Paralvinella bactericola</i>		x					Desbruyères and Laubier (1991)
<i>Paralvinella grasslei</i>		x			x		Desbruyères and Laubier (1982), Zal et al. (1995)
<b>Siboglinidae</b>							
<i>Riftia pachyptila</i>		x			x		Black et al. (1994)
<i>Escarpia spicata</i>	x	x*	x	x		x	Black et al. (1997), Levin et al. (2012a), Feldman et al. (1998), Tunnicliffe (1991)
<i>Lamelligibrachia barhami</i>	x		x	x	x		Black et al. (1997), Levin et al. (2012a)
<b>Hyalogyrinidae</b>							
<i>Hyalogyrina</i> sp.	x		genus	genus	genus	genus	Smith and Baco (2003), Bernardino et al. (2010), Smith et al. (2014), Sahling et al. (2002), Sasaki et al. (2010), Levin et al. (2012a)
<b>Associated macrofauna</b>							
<b>Nuculanidae</b>							
<i>Nuculana grasslei</i>	x	x					Allen (1993)
<b>Solemyidae</b>							
<i>Acharax</i> aff. <i>johnsoni</i>	x	x		x			Kamenev (2009)
<b>Hesionidae</b>							
<i>Sirsoe grasslei</i>	x	x					Blake and Hilbig (1990)
<b>Dorvilleidae</b>							
<i>Ophryotrocha platycephale</i>	x	x	x			x	Weiss and Hilbig (1992), Levin et al. (2003), Smith et al. (2014)
<i>Ophryotrocha akessoni</i>	x	x			x		Blake and Hilbig (1990)
<i>Parougia</i> sp.	x	x		genus	genus	genus	Smith and Baco (2003), Bernardino et al. (2010), Levin et al. (2003), Levin (2005), Smith et al. (2014)
<i>Exallopus jumarsi</i>	x	x					Petrecca and Grassle (1990)
<b>Polynoidae</b>							
<i>Branchinotogluma sandersi</i>	x	x			x		Blake and Hilbig (1990)
<i>Branchinotogluma hessleri</i>	x	x			x		Blake and Hilbig (1990)

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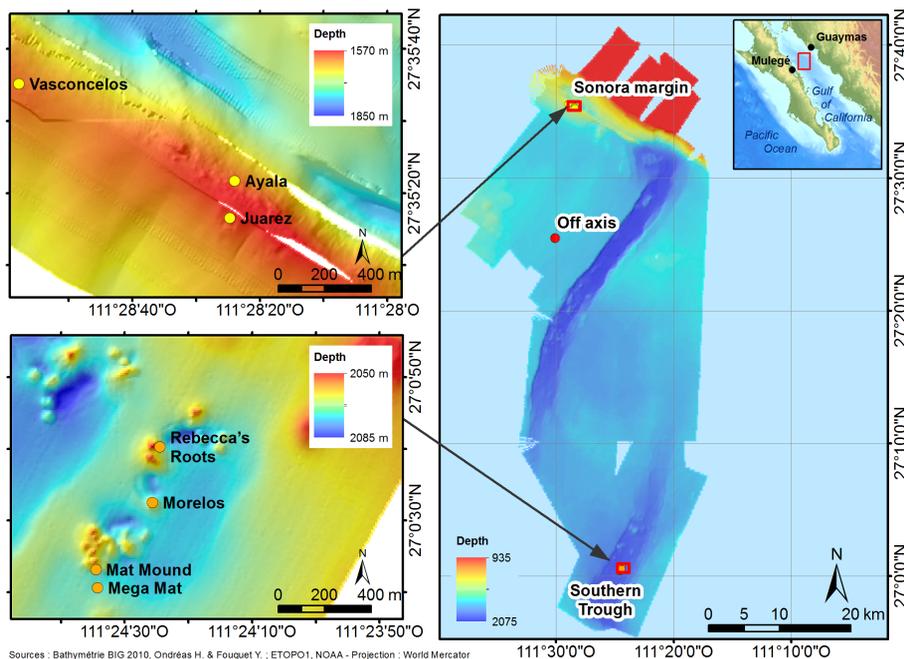
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Table 6. Continued.

	Guaymas	Guaymas	CRHS	CS	HV	OF	References
	Seep	Vent					
<i>Bathykurilla guaymasensis</i>	x	x				x	Pettibone (1993), Smith (2003), Blake and Hilbig (1990)
<i>Branchiplicatus cupreus</i>		x			x		Blake and Hilbig (1990)
<b>Nereididae</b>							
<i>Nereis sandersi</i>	x	x			x		Blake and Hilbig (1990)
<b>Maldanidae</b>							
<i>Nicomache venticola</i>	x	x			x		Blake and Hilbig (1990)
<b>Cirratulidae</b>							
<i>Aphelochaeta</i> sp.	x	x		genus			Levin et al. (2003)
<b>Pilargidae</b>							
<i>Sigambra</i> sp.	x	x		genus		x	Levin and Mendoza (2007), Dahlgren et al. (2004)
<b>Ampharetidae</b>							
<i>Amphisamytha</i> aff. <i>fauchaldi</i>	x	x	x	x			Stiller et al. (2013)
<b>Aplustridae</b>							
<i>Parvaplustrum</i> sp.	x	x					
<b>Provannidae</b>							
<i>Provanna</i> sp. (spiny)	x	x	x				Levin et al. (2012a)
<i>Provanna laevis</i>	x	x	x	x			Sahling et al. (2002), Sasaki et al. (2010), Smith and Baco (2003), Levin and Sibuet (2012b), Levin et al. (2012a), Warén and Bouchet (1993)
<b>Neomphaloidea</b>							
<i>Retiskenea diplooura</i>	x	x		x			Sahling et al. (2002), Sasaki et al. (2010)
Pyramidellidae							
<i>Eulimella lomana</i>	x	x*	x	x		x	Sahling et al. (2002), Sasaki et al. (2010), Smith and Baco (2003), Levin and Sibuet (2012b), Levin et al. (2012a), Warén and Bouchet (1993)
<b>Lepetodrilidae</b>							
<i>Lepetodrilus guaymasensis</i>	x	x	x				Levin et al. (2012a), Sasaki et al. (2010)
<b>Pyropeltidae</b>							
<i>Pyropelta corymba</i>	x	x	x	x		x	Sasaki et al. (2010), Levin et al. (2012a), Smith and Baco (2003)
<i>Pyropelta musaica</i>		x		x	x	x	Smith and Baco (2003), Tunnicliffe (1991), Sasaki et al. (2010)
<b>Neolepetopsidae</b>							
<i>Paralepetopsis</i> sp.	x			genus	genus	genus	Sasaki et al. (2010)
<b>Cataegidae</b>							
<i>Cataegis</i> sp.	x	x	genus	genus			Levin et al. (2012a), Sasaki et al. (2010)

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**Figure 1.** Localisation of the study sites on the Sonora margin cold seeps (Ayala, Vasconcelos and Juarez sites), the Southern Trough hydrothermal vents (Rebecca's Roots, Mat Mound, Morelos and Mega Mat sites) and the Guaymas Basin off-axis reference site.

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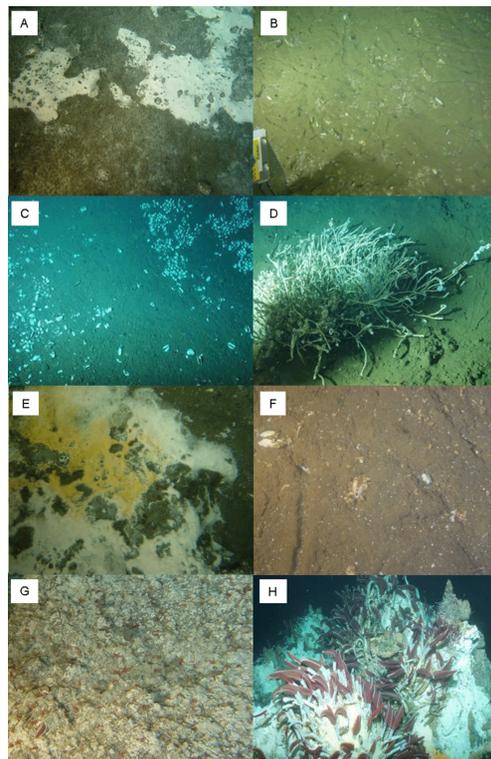
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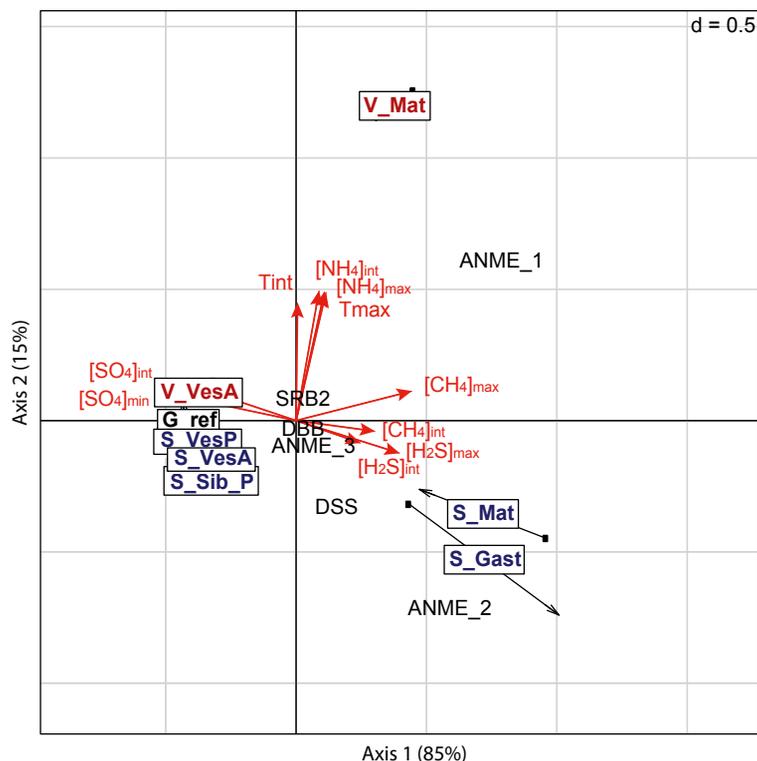
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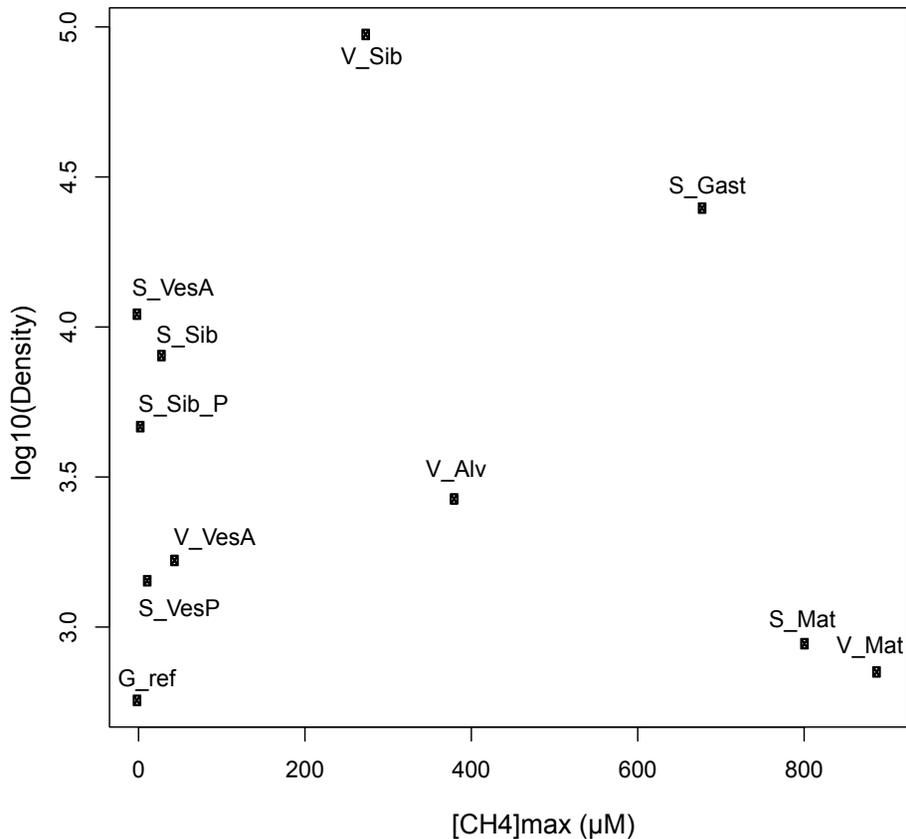
**Figure 2.** Images of studied assemblages at seeps: **(a)** *Beggiatoa* spp. microbial mat (S\_Mat) and *Hyalogyrina* sp. Gastropoda (S\_Gast), **(b)** *Archivesica gigas* Vesicomiyidae (S\_VesA), **(c)** *Phreagena kilmeri* Vesicomiyidae (S\_VesP), **(d)** *Escarpia spicata* and *Lamellibrachia barhami* Siboglinidae (S\_Sib) and their periphery (S\_Sib\_P) and vents: **(e)** *Beggiatoa* spp. microbial mat (V\_Mat), **(f)** *Archivesica gigas* Vesicomiyidae (V\_VesA), **(g)** *Paralvinella grasslei* and *P. bactericola* Alvinellidae (V\_Alv) and **(h)** *Riftia pachyptila* Siboglinidae (V\_Sib).

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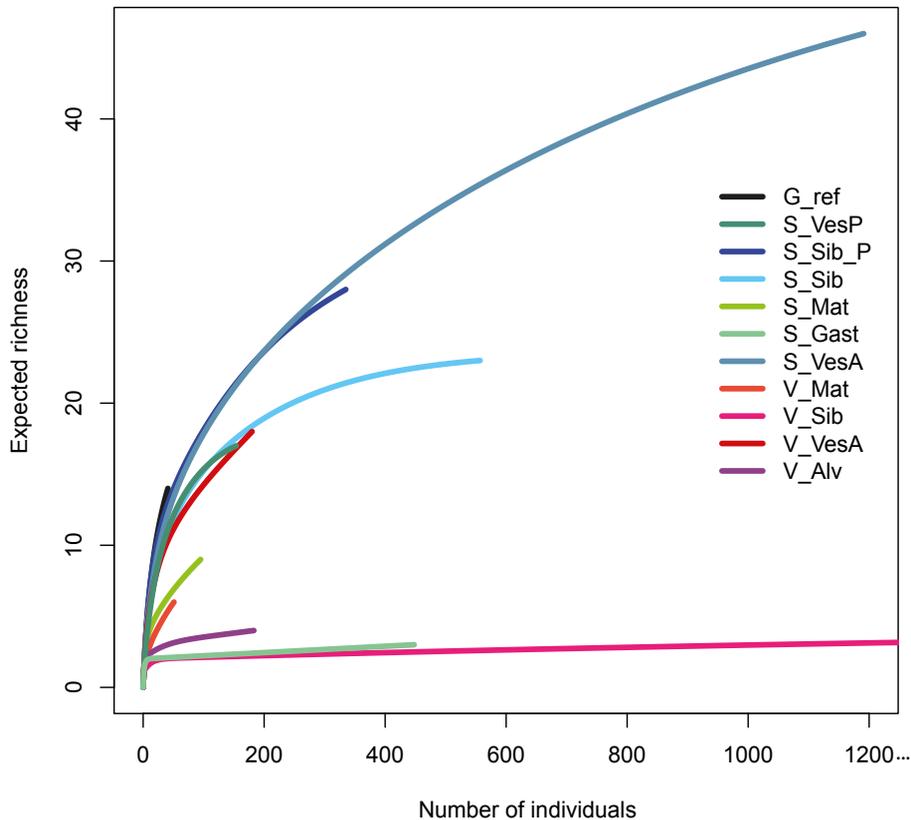
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**Figure 3.** Co-inertia analysis of physico-chemical factors in soft-sediment assemblages: temperature, methane ( $\text{CH}_4$ ), hydrogen sulphide ( $\text{H}_2\text{S}$ ), sulphate ( $\text{SO}_4$ ), ammonium ( $\text{NH}_4$ ) and relative abundances of microbial groups potentially involved in AOM: ANME1, ANME2, ANME3, DSS, DBB, SRB2.  $p = 0.01$ , Axis 1 accounts for 85% of the variation and Axis 2 represents 15%. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomidae (V\_VesA) and Microbial mat (V\_Mat).



**Figure 4.** Log-transformed macrofaunal densities according to maximum methane concentrations in assemblages. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomidae (V\_VesA) and Microbial mat (V\_Mat).



**Figure 5.** Rarefaction curves on pooled macrofaunal abundances from each assemblage. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), Siboglinidae (S\_Sib), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomidae (V\_VesA), Microbial mat (V\_Mat), Alvinellidae (V\_Alv) and Siboglinidae (V\_Sib).

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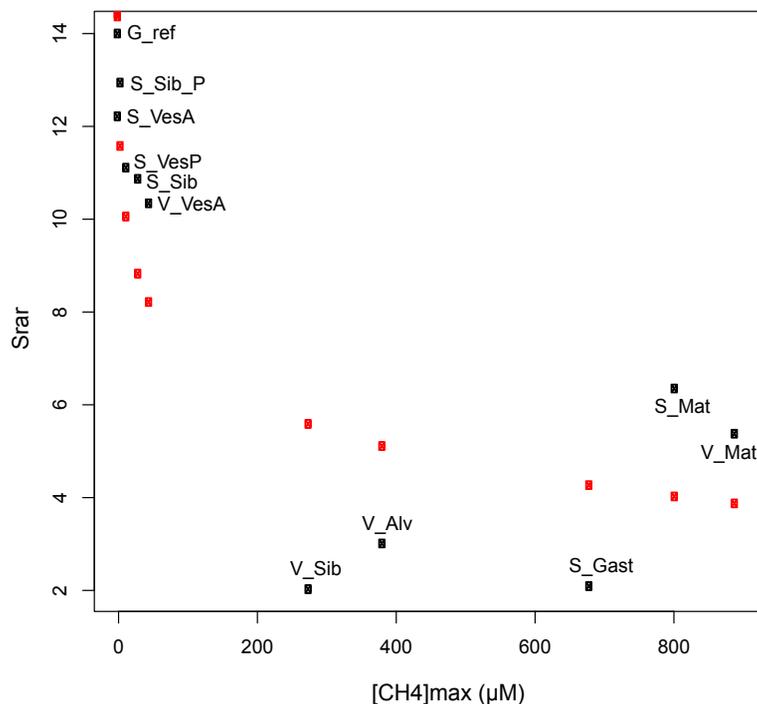
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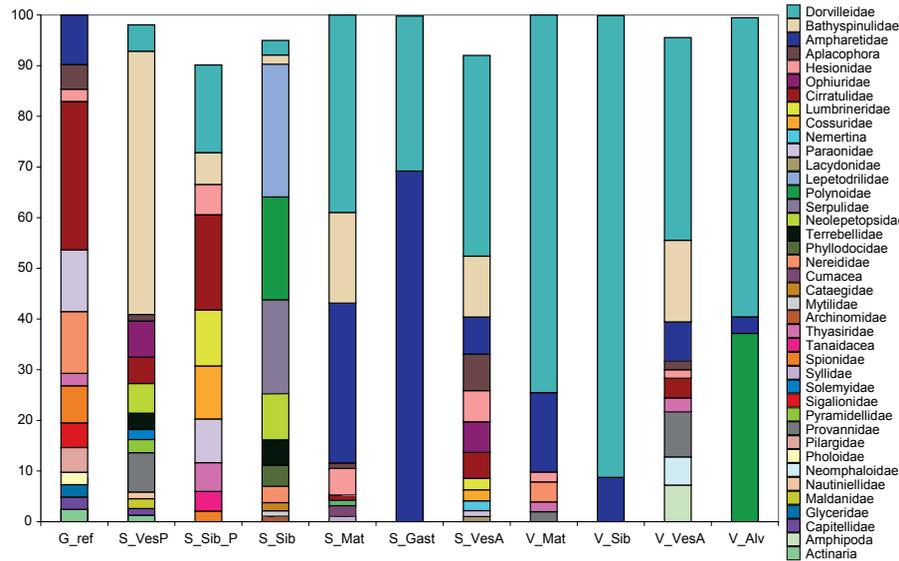


**Figure 6.** Logarithmic regression between species richness (ES(41), Srar) and maximum methane concentration in all macrofaunal assemblages. Black squares represent observed data points and red squares represent fitted values. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomidae (V\_VesA) and Microbial mat (V\_Mat).

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**Figure 7.** Histograms of relative macrofaunal compositions at the family level in assemblages shown for each study site, only taxa contributing to more than 1 % are shown. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), Siboglinidae (S\_Sib), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomidae (V\_VesA), Microbial mat (V\_Mat), Alvinellidae (V\_AlV) and Siboglinidae (V\_Sib).

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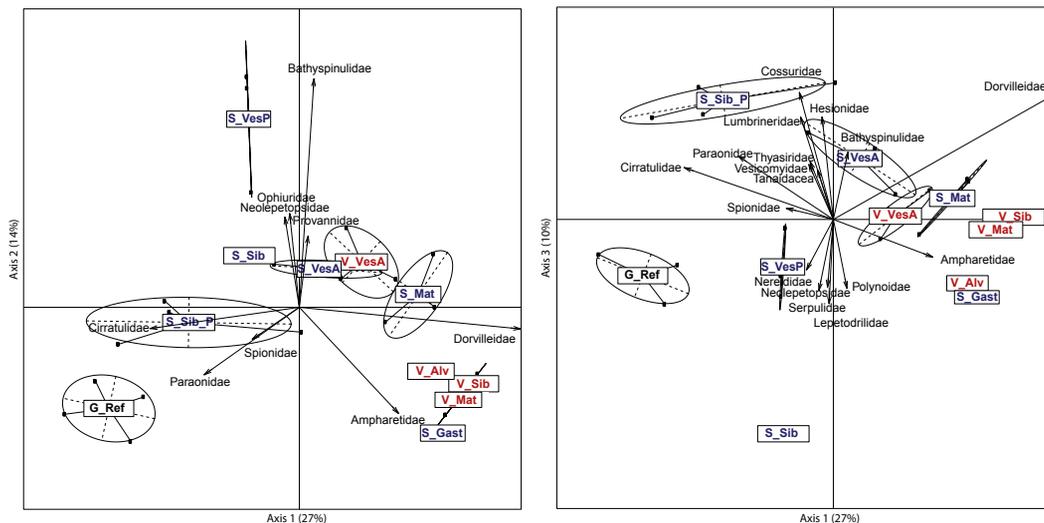
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**Figure 8.** Between-group principal component analysis (PCA) on Hellinger-transformed macrofaunal densities on the 26 sampling units studied in the Guaymas Basin. **(a)** The first axis accounts for 27% of the variance in the macrofaunal data and Axis 2 accounts for 14%. **(b)** The first axis accounts for 27% of the variance in the macrofaunal data and Axis 3 accounts for 10%. Only taxa contributing to more than 2% to either axis are shown. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), Siboglinidae (S\_Sib), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomidae (V\_VesA), Microbial mat (V\_Mat), Alvinellidae (V\_Aliv) and Siboglinidae (V\_Sib).

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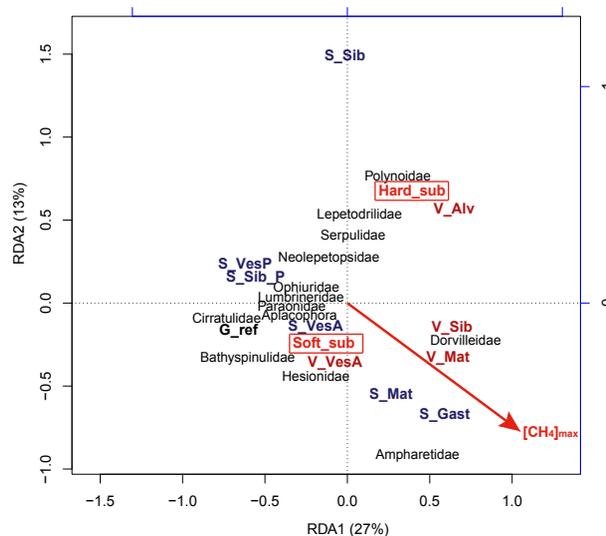
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**Figure 9.** Canonical redundancy analysis (RDA, scaling type 1) of Hellinger-transformed macrofaunal densities on all assemblages as a function of qualitative and normalised quantitative environmental conditions. Only significant explanatory variables are shown (methane concentration and substratum type). The first canonical axis represents 27 % of the total variance in macrofaunal abundance while the second axis represents 13 % (with an adjusted cumulated  $R^2$  of 0.25). The  $p$  value associated with the RDA1 axis is 0.01 and with the RDA2 axis, 0.08. Only the names of the taxa that showed good fit with the first two canonical axes (fitted value > 0.20) are shown on the plot. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomysidae (S\_VesP), *A. gigas* Vesicomysidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), Siboglinidae (S\_Sib), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomysidae (V\_VesA), Microbial mat (V\_Mat), Alvinellidae (V\_Alv) and Siboglinidae (V\_Sib).

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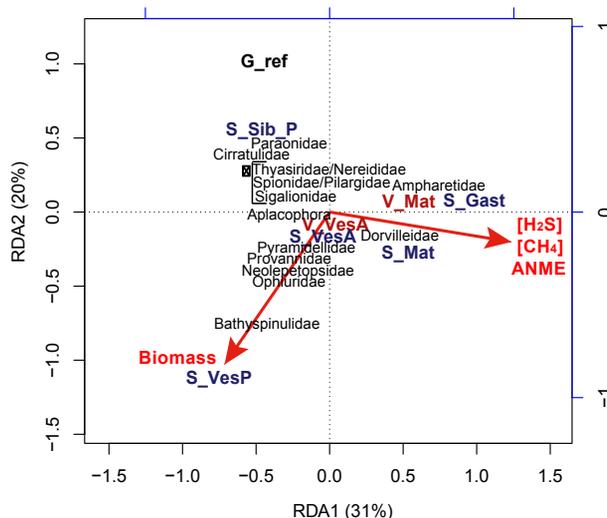
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**Figure 10.** Canonical redundancy analysis (RDA, scaling type 1) of Hellinger-transformed macrofaunal densities in soft-sediment assemblages as a function of normalized quantitative environmental conditions. Only significant explanatory variables are shown (First axis of the prior co-inertia analysis and engineer species biomass). The first canonical axis represents 31% of the total variance in macrofaunal abundance and the second axis represents 20% (with an adjusted cumulated  $R^2$  of 0.31). The  $p$  value associated with the RDA1 axis is 0.03 and with the RDA2 axis, 0.06. Only the names of the taxa that showed good fit with the first two canonical axes (fitted value > 0.20) are shown on the plot. REFERENCE: (G\_ref), SEEPS: *P. soyoae* Vesicomidae (S\_VesP), *A. gigas* Vesicomidae (S\_VesA), Microbial mat (S\_Mat), Gastropoda (S\_Gast), sediment at Siboglinidae Periphery (S\_Sib\_P) and VENTS: *A. gigas* Vesicomidae (V\_VesA), Microbial mat (V\_Mat).

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