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High connectivity across the fragmented chemosynthetic ecosystems of the deep Atlantic Equatorial Belt: efficient dispersal mechanisms or questionable endemism?

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Abstract

Chemosynthetic ecosystems are distributed worldwide in fragmented habitats harbouring seemingly highly specialized communities. Yet, shared taxa have been reported from highly distant chemosynthetic communities. These habitats are distributed in distinct biogeographical regions, one of these being the so-called Atlantic Equatorial Belt (AEB). Here, we combined genetic data (COI) from several taxa to assess the possible existence of cryptic or synonymous species and to detect the possible occurrence of contemporary gene flow among populations of chemosynthetic species located on both sides of the Atlantic. Several Evolutionary Significant Units (ESUs) of Alvinocarididae shrimp and Vesicomyidae bivalves were found to be shared across seeps of the AEB. Some were also common to hydrothermal vent communities of the Mid-Atlantic Ridge (MAR), encompassing taxa morphologically described as distinct species or even genera. The hypothesis of current or very recent large-scale gene flow among seeps and vents was supported by microsatellite analysis of the shrimp species *Alvinocaris muricola*/*Alvinocaris markensis* across the AEB and MAR. Two nonmutually exclusive hypotheses may explain these findings. The dispersion of larvae or adults following strong deep-sea currents, possibly combined with biochemical cues influencing the duration of larval development and timing of metamorphosis, may result in large-scale effective migration among distant spots scattered on the oceanic seafloor. Alternatively, these results may arise from the prevailing lack of knowledge on the ocean seabed, apart from emblematic ecosystems (chemosynthetic ecosystems, coral reefs or seamounts), where the widespread classification of endemism associated with many chemosynthetic taxa might hide wider distributions in overlooked parts of the deep sea.

Keywords: Atlantic equatorial belt, chemosynthetic habitats, deep-sea connectivity, endemic bivalves, endemic shrimp, genetic diversity, microsatellite markers, mitochondrial COI gene

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Introduction

Hydrothermal vents, cold seeps and other deep-sea sites of organic enrichment (whale- and wood-falls) have in common the use of reduced chemicals as energy source by chemoautotrophic bacteria that function as primary producers, allowing very high biomass production far from the euphotic zone (Desbruyères *et al.* 2000). Despite sharing chemoautotrophy for primary production of organic matter, chemosynthetic ecosystems differ in many characteristics. Hydrothermal vents, due to their tectonic and volcanic nature, are usually ephemeral and characterized by high temperatures, high sulphide and high heavy metal concentrations and are generally not strongly sedimented. In comparison,

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more stable and sediment-rich cold seeps are often associated with cold temperatures and diffusion of methane-rich fluids, harbouring more stable communities, which include species with extreme lifespan (Bergquist *et al.* 2000). Hydrothermal vents are scattered along mid-ocean ridges and back-arc spreading centres, while cold seeps are patchily distributed along active or passive margins associated with accumulated sediment. Despite their habitat differences, the chemosynthetic communities inhabiting these two kinds of ecosystems harbour common genera and sister species, suggesting a shared history of colonization during the evolutionary history of deep ocean habitats (Hecker 1985; McLean 1985).

Cold seeps, because of their distribution along continental margins, have been suggested as potential stepping-stone habitats for long-distance dispersal of vent species (Craddock *et al.* 1995). However, very few shared species have been detected among those ecosystems (Sibuet & Olu 1998; Baco *et al.* 1999; Tyler & Young 1999; Jollivet *et al.* 2000; Peek *et al.* 2000; Turnipseed *et al.* 2003; Andersen *et al.* 2004). One exception, supported by genetic analyses, is the vestimentiferan tubeworm *Escarpia spicata* found across different kinds of chemosynthetic habitats, namely cold seeps, whale falls and sedimented hydrothermal vents off the coast of California (Black *et al.* 1997). In the Northwestern Pacific, several morphologically determined species have been reported to occur in both seeps and vents; genetic connectivity between both ecosystems has been shown for *Lamellibrachia* tubeworms and *Bathymodiolus* mussels, but not for Vesicomyidae bivalves (Watanabe *et al.* 2010). Additionally, Vesicomyidae bivalves from whale carcasses in the Eastern Pacific have been shown to be genetically close to both seep (*Phreagena kilmeri*) and vent (*Archivesica gigas*) vesicomyids from the same region (Baco *et al.* 1999).

Since the discovery of these habitats in the mid-1970s, one of the most puzzling issues has been the influence of past and present connectivity on the nature of species assemblages and their geographical distribution (Corliss *et al.* 1979). Several studies to date have addressed the biogeography of vent ecosystems (Tunnicliffe 1997; Van Dover *et al.* 2002; Bachraty *et al.* 2009). The most recent assessment included 63 hydrothermal vents distributed worldwide and revealed the existence of five major biogeographical provinces: Mid-Atlantic Ridge (MAR), Indian Ocean, Western Pacific, Northeast Pacific Rise and East Pacific Rise, characterized by high levels of endemism, with 95% of the species not shared between provinces (Moalic *et al.* 2012). Cold seep ecosystems have been grouped into a few provinces: the Gulf of Mexico, Atlantic, Mediterranean, East Pacific and West Pacific (Tyler *et al.* 2003), with low species richness but high endemism (Tunnicliffe *et al.* 1998; Turnipseed *et al.* 2003).

The high levels of endemism currently reported for these ecosystems indicate that vent fauna have in general low dispersal potential, although taxonomic uncertainty might cause an overestimation of endemism (Vrijenhoek 2009). Because access to great depths is extremely challenging, there is insufficient information about species variation in space and time. This knowledge gap might lead to the description, across sites and provinces, of synonymous species (morphologically distinct yet belonging to a single interbreeding species) or on the contrary, single species descriptions including undetected cryptic ones (morphologically indistinguishable but reproductively isolated species). To date, population genetics analyses have surprisingly shown a generally high capacity for long-distance dispersal and gene flow for organisms associated with chemosynthetic habitats (Peek *et al.* 2000; Kyuno *et al.* 2009; Vrijenhoek 2010; Teixeira *et al.* 2011a, 2012; Thaler *et al.* 2011; Van der Heijden *et al.* 2012), except for some cases of genetic differentiation (Jollivet *et al.* 1995; Hurtado *et al.* 2004; Johnson *et al.* 2006; Plouviez *et al.* 2009). Thus, whether the high endemism reported among seeps and vents reflects speciation and lack of connectivity among habitats or is partly overestimated by descriptions of synonymous species due to morphological plasticity requires further in-depth investigations (Samadi *et al.* 2006; Vrijenhoek 2009).

The Atlantic equatorial belt (AEB) has been identified as one of the areas of choice to study connectivity among deep chemosynthetic ecosystems (Tyler *et al.* 2003). Seep communities have been described along the American and African margins (e.g. Olu *et al.* 1996, 2009; Cordes *et al.* 2007) potentially connected through equatorial currents. Genetically and morphologically similar taxa of Bathymodiolinae mussels were found at seeps from both sides of the Atlantic, raising questions about the past and/or present-day connection along the AEB (Olu-Le Roy *et al.* 2007). A hypothetical west-east passage has been proposed for chemosynthetic species across the equatorial Atlantic, with a possible role of hydrothermal vents distributed along the transform faults of the MAR as conduits to dispersal (Van Dover *et al.* 2002; Tyler *et al.* 2003). The most recent biogeographical analysis of taxa across the AEB showed that communities cluster according to depth rather than geographical distances (Olu *et al.* 2010). Among 72 taxa, only nine species appeared to be present on both sides of the Atlantic, and the hypothesis of the MAR hydrothermal vents acting as stepping stones for migration between both sides was not supported. Sister species of mussels of the genus *Bathymodiolus* are segregated among different types of chemosynthetic ecosystems.

This is also the case for shrimp, with *Alvinocaris muricola* occurring at cold seeps on both sides of the Atlantic and its sister taxa *Alvinocaris markensis* occurring at vents along the MAR (Olu *et al.* 2009). However, the presence of *A. muricola* was once suspected in the Logatchev site of MAR (T. Shank, personal cummunication in Komai & Segonzac 2005). More recently, the Vesicomyidae bivalves *Calyptogena* sp. and *Vesicomya* sp., now re-named *Abyssogena southwardae* (Audzijonyte *et al.* 2012), were recorded for both Western Atlantic seeps and vents of the MAR, based on morphological traits (Krylova *et al.* 2010), and also genetic similarities (at the mitochondrial cytochrome oxydase subunit I, COI; Decker *et al.* 2012; Van der Heijden *et al.* 2012).

To test the hypothesis of large-scale dispersal between seeps and vents of the Atlantic equatorial belt, we used partial sequences of the mitochondrial cytochrome oxidase subunit I (COI) gene from several morphologically described species of Alvinocarididae shrimps and Vesicomyidae bivalves. To obtain estimates of gene flow across the Atlantic equatorial belt, the shrimp taxa (*Alvinocaris* sp.) identified as shared among sites on the basis of COI sequence analysis were then further analysed using the nuclear 18S ribosomal RNA gene (18S rRNA) and nine microsatellite markers.

Materials and methods

Sampling and DNA extraction

The Alvinocarididae shrimp and Vesicomyidae bivalve taxa analysed in this study were collected from cold seeps of the Eastern (Congo margin) and Western (Gulf of Mexico) Atlantic and from hydrothermal vents (along the Mid-Atlantic Ridge—MAR) during several oceanographic cruises. Three cold seep areas along the Congo margin were sampled during the WACS and the Congolobe cruises including the Regab and the Worm Hole pockmarks (Ondréas *et al.* 2005; Sahling *et al.* 2008). The terminal lobes of the Congo deep-sea fan, a sedimentary zone where chemosynthetic species are present, were also sampled during these cruises (Sibuet & Vangriesheim 2009). Shrimp samples were collected using a slurp-gun from the Remotely Operated Vehicle (ROV) Victor or the manned submersible Nautile, and Vesicomyidae bivalves were mainly collected with nets and sometimes embedded in sediment cores. Prior to each dive, the bowls used for collecting the shrimp were aseptically washed with ethanol (96%) before being filled with sterile seawater; the nets and cores were similarly cleaned. Once on board, live specimens were either frozen whole or immediately dissected into body parts under sterile conditions and frozen or preserved in 70% alcohol. DNA extraction was performed using the CTAB (cetyl trimethyl ammonium bromide) method (Doyle & Doyle 1990) on muscle tissue. Sample sizes are described in Table 1.

Taxon sampling of the Vesicomyidae bivalves included five described species of *Abyssogena*: *Abyssogena kaikoi* Okutani and Metivier 1986, Nankai Trough; *A. mariana* Okutani *et al.* 2013; from the Shinkai seeps; *A. phaseoliformis* Metivier *et al.* 2006, Kurile Trench; *A. novacula* Krylova *et al.* 2010; from Peru trench seeps; and *A. southwardae* Krylova *et al.* 2010; Barbados Accretionary Prism, West Florida Escarpment and Logatchev vent field. We also included an undescribed *Abyssogena* specimen, from Ryukyu Trench Kojima *et al.* 2004.

As GenBank contains data obtained prior to the new taxonomic revision, and/or unnamed/re-identified sequences, we have renamed these sequences (see Table 1) according to their identification in the most recent taxonomic revision (Audzijonyte *et al.* 2012). This new nomenclature was used throughout the analysis.

In addition, sequences available in GenBank for morphologically identical or closely related species (Table 1) were integrated in the analysis to define clusters of identical or highly similar groups of sequences or taxa that would support or challenge morphological taxonomy or identification. All species analysed and their locations are detailed in Fig. 1 and Table 1. Based on our sequence results (see Results below), the Alvinocarididae shrimp were grouped into two Evolutionary Significant Unit (ESU), and one of these (hereafter referred to as ESU 1) was further investigated with more detailed microsatellite analyses (sample size permitting this analysis).

Polymerase chain reaction, sequencing and genotyping

Part of the mitochondrial COI gene, the 18S gene (ca 1.7 kb) and nine microsatellite loci were amplified according to the conditions detailed in Table 2. The PCR amplifications were conducted on a Perkin-Elmer Gene Amp System 7200 (Waltham, MA, USA). PCR products obtained for the mitochondrial and the 18S gene were sent to be purified and sequenced commercially at Macrogen, Inc. (Seoul, Korea) and GATC Biotech (Konstanz, Germany), while microsatellite fragments were separated on an ABI 3130 XL automatic sequencer with the internal size standard Rox 350. Alleles were scored using PEAK SCANNER version 1.0 (Applied Biosystems).

Data analysis

Phylogenetic reconstruction. Alignments of nucleotide sequences were constructed with CLUSTAL X version 1.83 using the default parameters (Thompson *et al.* 1997)

Table 1 GenBank accession numbers, specimen collection sites and depth of species used for phylogenetic analyses

Specimen	Nomenclature according to Audzijonyte *et al.* 2012	Accession no.	Sample site	Area	Habitat	Depth (m)	Study; sample size
Bivalves							
Abyssogena southwardae		\JX900981; \JX901014	WormHole pockmark	East Atlantic	Seep	3089	This study; 2
A. southwardae		\JX900982-\JX901013	Lobes of the Congo deep-sea fan	East Atlantic	Presumably Seep	4946	This study; 32
Calyptogena kaikoi	*Abyssogena kaikoi*	\AB110763	Off Muroto Point, Nankai Trough	Western Pacific	Seep	4800	Kojima *et al.* 2004
Vesicomyidae sp. 'Ryukyu Trench'	*Abyssogena* sp. Ryuku	\AB110775	Ryukyu Trench	Western Pacific	Seep	5900	Kojima *et al.* 2004
Calyptogena sp. 6K1234-1/2	*Abyssogena mariana*	\AB629938/39	Shinkai Seep Field	Western Pacific	Vents	5550	Ohara *et al.* 2012; Okutani *et al.* 2013
Calyptogena phaseoliformis	*Abyssogena phaseoliformis*	\AB479088	Kurile Trench	Western Pacific	Seep	4819	Okutani *et al.* 2009
Calyptogena sp.	*A. southwardae*	\AF008279; \JX196983	Barbados Accretionary Prism	Western Atlantic	Seep	5000	Peek & Gustafson 1997; Audzijonyte *et al.* 2012
Calyptogena n. sp. *West Florida Escarpment*	*A. southwardae*	\AF008280	West Florida Escarpment	Western Atlantic	Seep	3313	Peek & Gustafson 1997
Vesicomya sp. MAR	*A. southwardae*	\EU403471	Logatchev	Mid-Atlantic Ridge	Vent	3028	Stewart *et al.* 2008
A. southwardae		\JQ844786; \JQ844787	Clueless	Mid-Atlantic Ridge	Vent	2995	Van der Heijden *et al.* 2012
Abyssogena novacula		\JX196970	Peru Trench	Pacific	Seep	5528	Van der Heijden *et al.* 2012
Calyptogena nautilei	« Undetermined genus » *nautilei*	\AB110759	Zenisu Ridge, Japan	Western Pacific	Seep	3300	Kojima *et al.* 2004
Arthropods							
Alvinocaris muricola		\KC840887- \KC840892; \KC840894	Gulf of Mexico, GC852 site	Western Atlantic	Seep	1450	This study; 12
Alvinocaris markensis		\KC840879- \KC840886; \KC840893	Logatchev	Mid-Atlantic Ridge	Vent	3028	This study; 11
A. markensis		\AF125408/409	Snake Pit	Mid-Atlantic Ridge	Vent	3398	Shank *et al.* 1999
Alvinocaris aff. *muricola*		\KC840895- \KC840927	Regab, West Africa	East Atlantic	Seep	3157	This study; 78
Alvinocaris methanophila		\AY163260	Blake Ridge	Western Atlantic	Seep	2155	Van Dover *et al.* 2002
Chorocaris chacei		\KC840932- \KC840940	Lucky Strike	Mid-Atlantic Ridge	Vent	1700	This study; 80
C. chacei		\KC840928- \KC840931	Logatchev	Mid-Atlantic Ridge	Vent	3028	This study; 16
Rimicaris hybisae		\JN850607	Mid-Cayman Ridge	Western Atlantic	Vent	4960	Nye *et al.* 2012

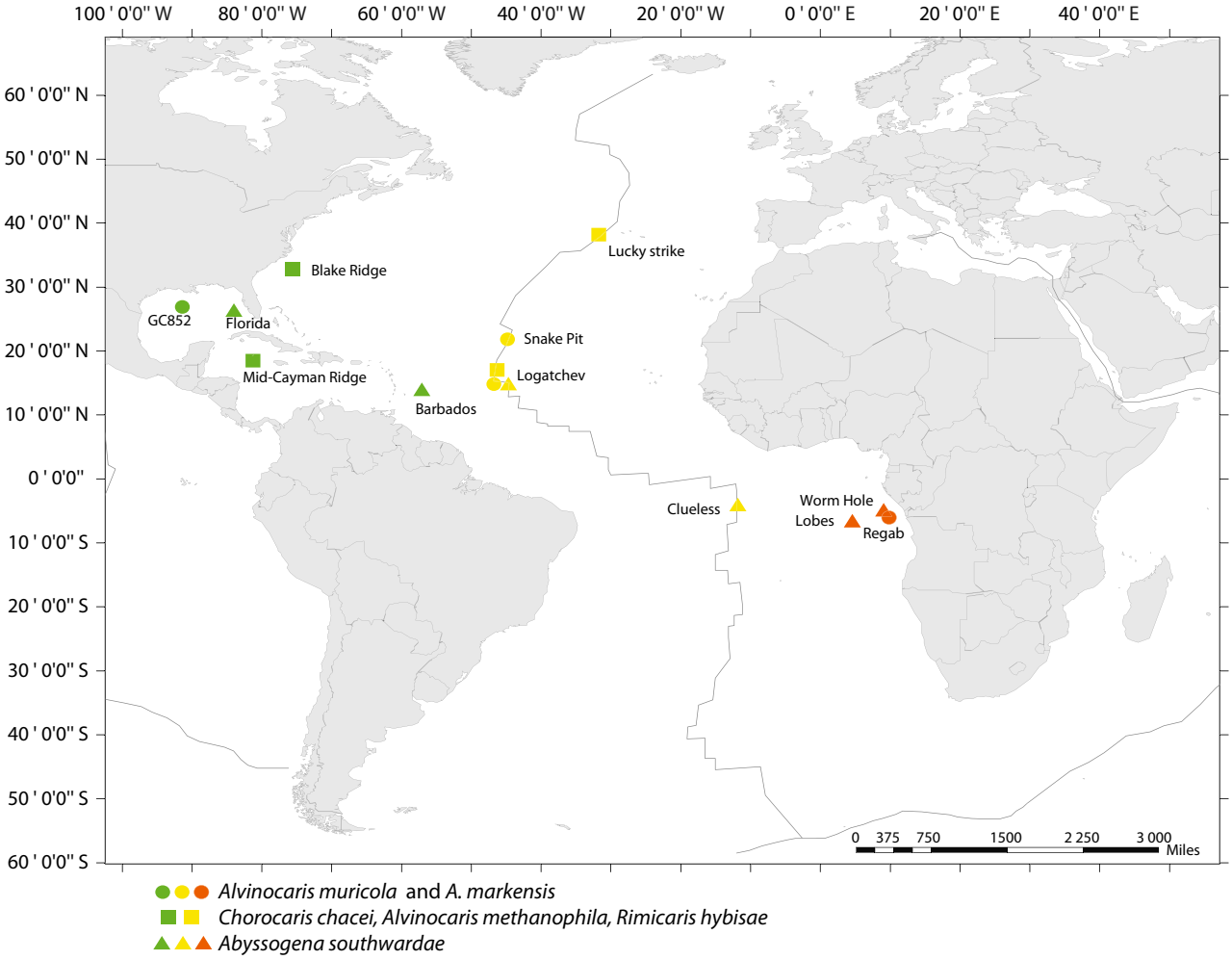

Fig. 1 Location of the specimens and populations sampled across the Atlantic Equatorial Belt (AEB). Legend: Triangles- *Abyssogena southwardae*; circles - species comprised in ESU1 (*Alvinocaris muricola* /*A. markensis*); squares - species comprised in the ESU2 (*Chorocaris chacei*, *Alvinocaris methanophila* and *Rimicaris hybisae*). Colour codes: Green - Western Atlantic; Yellow - Mid-Atlantic Ridge; Orange - Eastern Atlantic.

Table 2 Details of primers and PCR conditions used for the different molecular markers amplified

	Cytochrome Oxydase subunit I (Folmer *et al.* 1994)	18S rRNA (López-García *et al.* 2003)	Microsatellites (Zelnio *et al.* 2010; Teixeira *et al.* 2011b)
Primer names	LCOI1490; HCOI2198	18S–82F; 18S–1498R	Rim 11; 12; 26; 30; 32; 42; CHO 83; 91
DNA (ng)	50	50	10
$MgCl_2$ (mM)	2.5	3	3
dNTP (mM)	0.8	0.8	0.8
Taq (U/μL)	0.4	0.4	0.5
Final volume (μL)	50	20	10
Annealing temperature (°C)	52	56	(Zelnio *et al.* 2010; Teixeira *et al.* 2011b)

and verified by eye to maximize positional homology. Only unique haplotypes were included in phylogenetic analyses.

Three different data sets were analysed: (i) partial sequences of the COI gene of 26 Vesicomyidae bivalves (14 from this study) using 'undetermined genus' *nautilei* (former *Calyptogena nautilei*) as the outgroup produced an alignment of 502 bp; (ii) partial sequences of the COI gene of 39 Alvinocarididae shrimps (35 from this study) using *Stenopus hispidus* as the outgroup produced an alignment of 447 bp; and (iii) partial sequences of the nuclear 18S rRNA gene of 20 Alvinocarididae shrimps

(17 from this study) using *Eugonatonotus chacei* as the outgroup produced an alignment of 483 bp.

Prior to the phylogenetic reconstructions of the Alvinocarididae shrimp, we obtained an initial data set of 198 Alvinocarididae partial COI sequences (28 retrieved from the GenBank representing all available deep-sea chemosynthetic shrimp species), of which we discarded all identical and all highly dissimilar sequences (clustered with ours with a divergence level higher than 4%), this approach resulted in the final phylogenetic data set of 39 COI sequences analysed.

The nuclear 18S rRNA data set included three *Alvinocaris aff. muricola* from West African seeps, four *A. muricola* from the Gulf of Mexico seep, six *A. markensis* from the Logatchev vent field and four *Chorocaris chacei* from Lucky Strike vent field. Two sequences retrieved from GenBank: *A. muricola* and *Rimicaris hybisae* were also included in the nuclear data set (accession numbers detailed in Fig. 4).

The Akaike information criterion (Akaike 1973) implemented in MODELTEST v.3.7 (Posada & Crandall 1998) was used to determine the evolutionary models that best fit each of the three data sets. PHYML v2.4.4 (Guindon & Gascuel 2003) was used to estimate the maximum-likelihood (ML) trees in all data sets and to test by nonparametric bootstrap proportions (BPs) the robustness of the inferred trees using 1000 pseudoreplicates. The selected model for the COI Alvinocarididae data set used in ML analysis was the GTR + Γ, whereas the JC was the selected model for the nuclear data set. The best-fit evolutionary model for the Vesicomyidae COI data set was the TrN + I. All ML analyses were carried out on the freely available Bioportal (http://www.bioportal.uio.no).

Bayesian inferences (BI) were conducted with MRBAYES v3.1.2 (Huelsenbeck & Ronquist 2001) by Metropolis coupled Markov chain Monte Carlo (MCMCMC) analyses were run for four million generations and sampled every 100 generations. Two independent runs were performed to reduce chances in selecting a local but not a global optimum. The burn-in was set to 2 000 000 generations, and robustness of the inferred trees was evaluated using Bayesian posterior probabilities (BPPs).

The Alvinocarididae shrimp COI data set was analysed under the GTR + Γ (Nst = 6), the best-fit model for the nuclear data set was JC (Nst = 1), and the Vesicomyidae bivalve COI data set was analysed under the TrN + I (Nst = 6). All Bayesian analyses were performed on the CCMar Computational Cluster Facility (http://gyra.ualg.pt) at the University of Algarve.

To analyse and illustrate the divergence levels among haplotypes found for the Vesicomyidae bivalves and Alvinocarididae shrimp across sites, median-joining networks were constructed, using the number of mutations as distance, using Network v. 4.1.0.9 (Bandelt *et al.* 1999) to infer the most parsimonious branch connections between the sampled haplotypes. In this analysis, higher sample sizes (all available sequences) were used in relation to the ML trees obtained for both organisms (bivalves and shrimp). For the network analysis, a total of 44 sequences were used to obtain one haplotype network of *A. southwardae* (details in Table 1), while for the Alvinocarididae shrimp, a total of 199 sequences were used to obtain two haplotype networks (corresponding to ESU 1 and 2; Fig. 3), 197 sequences were generated in this study (as explained in the sampling section) and two sequences retrieved from GenBank (*R. hybisae* and *Alvinocaris methanophila*). To obtain the haplotype network corresponding to ESU 1, 101 sequences were used (all generated in this study), and for the network corresponding to ESU 2, 98 sequences were used (two of these were retrieved from GenBank as explained above).

Atlantic equatorial belt connectivity of Alvinocaris shrimp (ESU 1). The clade we named ESU 1 (Fig. 3), which includes *A. muricola* (from West Africa and Gulf of Mexico seeps) and *A. markensis* (Logatchev vent field), had enough sequences available for further analyses (101 individuals, see Results section for details). These were analysed using ARLEQUIN version 3 (Schneider *et al.* 2000) to estimate gene diversity and conduct statistical tests on mitochondrial (COI) data.

For each sampling location, the following statistics were computed for mitochondrial data: number of private haplotypes (*N*ph), haplotype (*h*) and nucleotide diversities (π_2) (Nei 1987), and mean number of pairwise differences (π_1) (Tajima 1983). To assess population differentiation, pairwise F_{ST} values were calculated following the method of Hudson *et al.* (1992), and exact tests of differentiation were conducted following the method of Raymond & Rousset (1995).

For demographic analysis, we determined Fu's F_S (Fu 1996) and Tajima's D (Tajima 1989), which can detect departures from selective neutrality and changes in population size such as expansions or bottlenecks (Tajima 1996; Fu 1997). Both statistics are expected to result in negative values after a population expansion (Ray *et al.* 2003) or a selective sweep, whereas positive values are expected under balancing selection of recent bottlenecks.

To assess asymmetrical gene flow between the seeps and vent sampled, we used MIGRATE version 3.2.16 (Beerli 2009). This analysis is based on ML estimates for both migration rates and effective population sizes using a coalescent approach (Beerli & Felsenstein 1999). We used an initial random seed number and θ and *M* starting parameters calculated from F_{ST}. As searching strategy,

we used 40 short chains (4000 trees sampled) and six long chains (40 000 trees sampled). For each chain, the first 300 000 steps were used as a burn-in, and adaptive heating was used to ensure an independent, comprehensive search of the parameter space. We performed four independent runs and verified their congruence.

For the microsatellite data (nine loci used), the mean number of alleles per locus (allelic diversity), the expected (H_E) and observed (H_O) proportion of heterozygotes, and the inbreeding coefficient (F_{IS}) were estimated using GENETIX 4.05 (Belkhir *et al.* 1996). Significance levels were estimated using a permutation approach (1000 permutations). The software GENCLONE (Arnaud-Haond & Belkhir 2007) was used to calculate standardized allelic richness (A_{rich}), to compensate for the unequal sample sizes.

The *F* estimator of genetic structure θ (Weir & Cockerham 1984) was calculated for each locus and over all loci. The probability of the *F*-statistics being greater than zero was determined by permutation (10 000 replicates) using GENETIX 4.05 (Belkhir *et al.* 1996). Correction for multiple testing was performed using the false discovery rate (FDR) approach (Benjamini & Hochberg 1995) in the software QVALUE (Storey 2002).

To test for a reduction in effective population size linked to bottleneck or founder events, the Wilcoxon sign-rank test was applied to test for differences between heterozygosities estimated from allele frequencies (H_E) and from the number of alleles and sample size (H_{Eq}). During a bottleneck, allele number decreases faster than heterozygosity, resulting in a transient apparent heterozygosity excess, indicative of a recent bottleneck event (Cornuet & Luikart 1996), whereas the opposite (allele excess) might occur during a population expansion (Maruyama & Fuerst 1984). Tests were implemented by BOTTLENECK 1.2.02 (Cornuet & Luikart 1996) using 1000 iterations. Estimates of H_{Eq} were calculated under the single-step mutation model (SMM) and the two-phase model (TPM), allowing for 10% multi-step mutations.

Results

Vesicomyidae bivalves

Potential Scale Reduction Factors in Bayesian analyses (all data sets) were 1.00, indicating full convergence of the runs (Gelman & Rubin 1992). Phylogenetic relationships within the genus *Abyssogena* were mostly unresolved, and only two well-supported clades were recovered in both the ML and BI analyses (Fig. 2): one corresponded to *A. mariana* from the Shinkai Seep Field (Pacific Ocean), and the other clade included the samples of *A. southwardae* from the Lobes of the Congo deep-sea fan and West Florida Escarpment. Sequence divergence between the 20 individuals of *A. southwardae* collected at the Western, Eastern and MAR was very low (less than 1.2% maximum divergence). These clustered into three groups that were geographically mixed and poorly statistically supported.

No identical sequences of *A. southwardae* were detected among those available in GenBank for Western Atlantic cold seeps (Florida Escarpment and Barbados Accretionary Prism), MAR (Logatchev vent field) nor the ones generated in this study from Eastern Atlantic cold seeps (Western Africa cold seeps). However, the haplotypes from Florida Escarpment and MAR appear in a central position in the network, intermediate between several haplotypes retrieved from Western African cold seeps (Fig. 5). While the two Barbados samples of *A. southwardae* (JX196983; AF008279) displayed a large divergence between themselves (five point mutations); the JX196983 sequence appeared in the haplotype network between the AF008279 sequence and the other *A. southwardae* sequences of the MAR. The JX196983 sequence displayed 1 point mutation divergence from the MAR and 2 point mutations divergence from the Florida *A. southwardae*. Of the 20 *A. southwardae* sequences analysed of the Atlantic ocean, the AF008279 Barbados sequence was the most divergent (1.2% maximum divergence).

Alvinocarididae shrimp

Potential Scale Reduction Factors in Bayesian analyses (all data sets) were 1.00, indicating full convergence of the runs (Gelman & Rubin 1992). Both the ML and BI trees based on the COI gene obtained from several Alvinocarididae shrimp species exhibited two well-supported and very divergent clades (Fig. 3). The first clade, which we call ESU 1 (Evolutionary Significant Unit 1, Fig. 3), includes all *A. muricola* and *A. markensis* from seeps and vents of the Atlantic. The second clade (ESU 2, Fig. 3) includes specimens with sequence divergence bellow 2%. This comprises *C. chacei* from the MAR vents, the newly described *R. hybisae* (which shares some identical sequences with *C. chacei* but still displayed a maximum divergence of 0.8%) from the Cayman Ridge vents and *A. methanophila* (1.4% divergence with *C. chacei*) from Blake Ridge seeps. In accordance with these results, the ML tree obtained using the 18S gene clusters the same taxa as the COI gene for the second clade (ESU 2) with high support (Fig. 4), while it lacked resolution in the first clade (ESU 1; Fig. 4).

In ESU 2 (*Chorocaris/Rimicaris/A. methanophila*), 15 distinct haplotypes were recovered (Fig. 5) of the 98 sequences analysed for COI. Of these, 10 haplotypes were unique (66.7%) and the remaining five that were

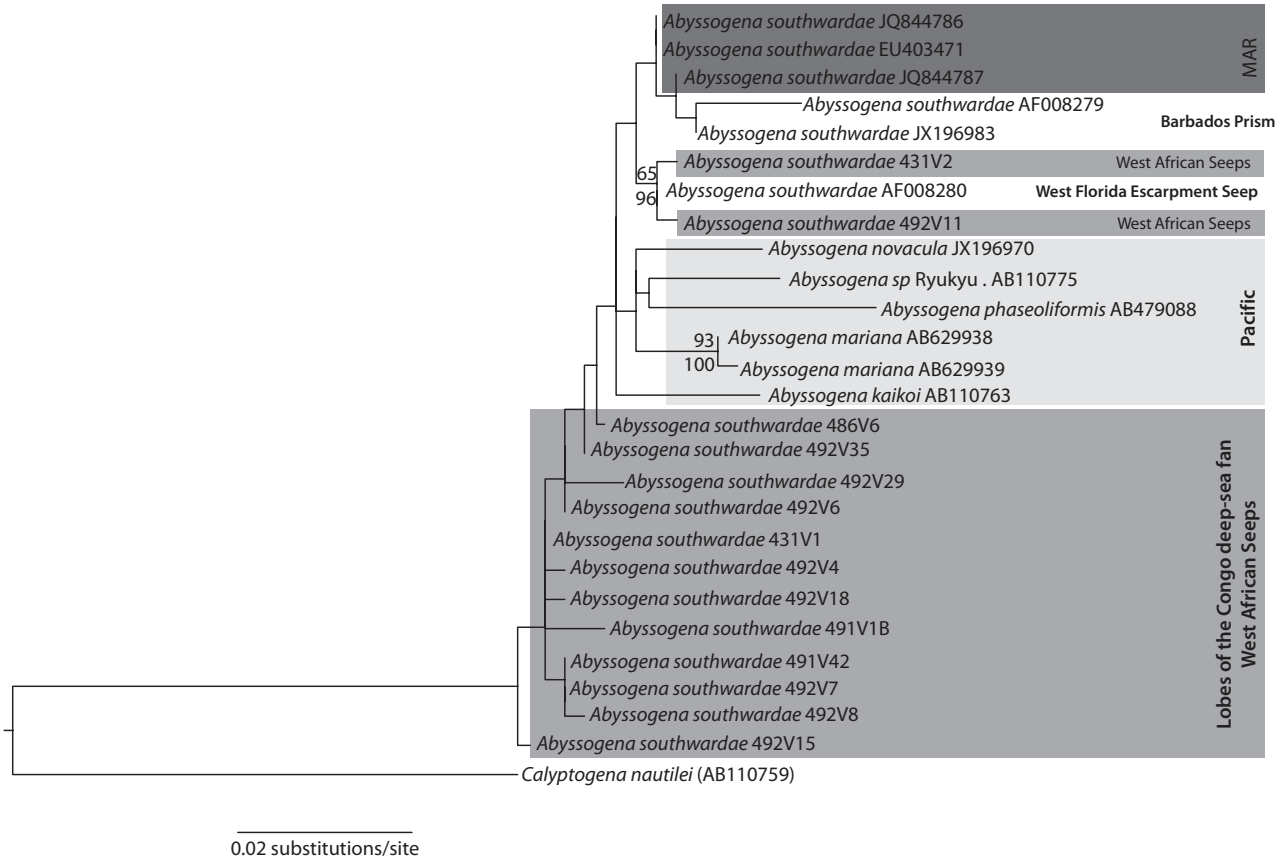

Fig. 2 Phylogenetic relationships of the *Abyssogena* bivalves based on the maximum-likelihood (ML) analysis of partial sequence data of the mitochondrial COI gene using the TrN + I evolutionary model.

shared, that is, haplotypes displayed by more than one individual, belonged to *C. chacei* from the Logatchev and Lucky Strike vent fields (accession numbers \KC840928 to \KC840940). The *R. hybisae* sequence had only one point mutation from a *C. chacei* haplotype and only two point mutations from the most common haplotype. Similarly, the results for the 18S gene also revealed very low divergence between *R. hybisae* and *C. chacei* (0–0.4% divergence). The *A. methanophila* haplotype was more distant from the centre of the haplotype network, with eight point mutations from the most common haplotype (Fig. 5). Yet, the ML tree (Fig. 3) clusters this specimen in ESU 2 making the genus *Alvinocaris* (ESU 1) non-monophyletic, an issue that should be verified with nuclear sequence data.

Population analysis. For the ESU 1 clade, which had sufficient sampling size for a population analysis, a total of 49 haplotypes were recovered of the 101 individuals analysed, all belonging to the genus *Alvinocaris* (*A.* aff. *muricola* from West African seeps, *A. muricola* from the Gulf of Mexico seep and *A. markensis* from the Logatchev vent field; Fig. 5) sampled across the Atlantic Equatorial Belt (AEB). A total of 45 (91.8%) haplotypes were 'private' (Fig. 5; accession numbers: \KC840879 to \KC840927). The most common haplotype was present in all populations sampled across the whole study region and was central to all other haplotypes, most of these represented by a single individual and divergent by a single or double point mutation, leading to the central haplotype as the core of a starlike topography (Fig. 5).

Haplotype diversity (h) was high for all populations, ranging from 0.80 (West Africa seeps, $n = 78$) to 0.96 (Logatchev vent, $n = 11$). In contrast to these rather high values of haplotype diversity, nucleotide diversity (π_2) was, however, low, ranging from 0.0037 to 0.005 (Table 3).

Multilocus genotypes at the nine microsatellite loci analysed for 98 *Alvinocaris* shrimp (ESU1) from the three sites across the Atlantic equatorial belt (*A. muricola* from the Gulf of Mexico and West Africa and *A. markensis* from Logatchev) also revealed high genetic diversity. The mean number of alleles per locus increased with sample size (Table 4), but the standardized allelic richness (A_{rich}) did not show major trends, ranging from 4.67 (Logatchev) to 5.47 (Gulf of Mexico).

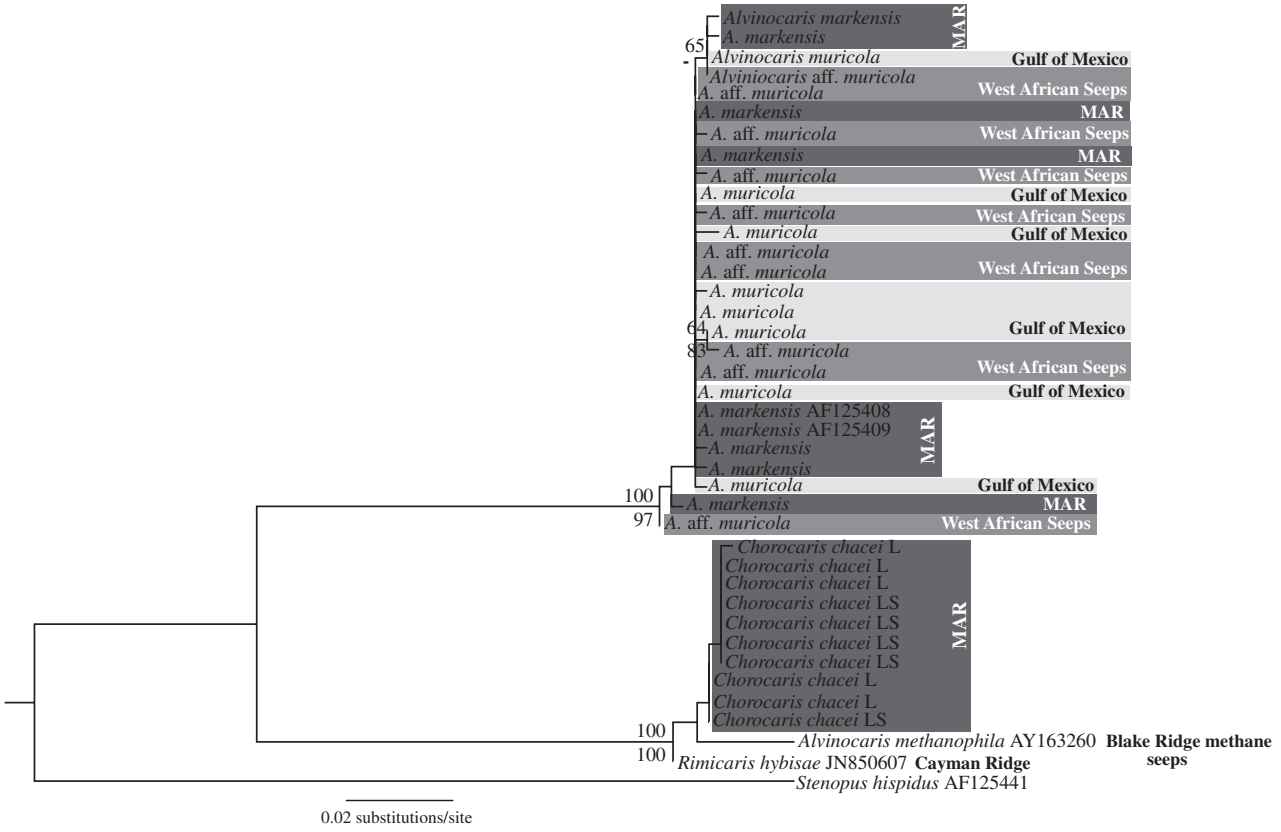

Fig. 3 Phylogenetic relationships of Alvinocarididae shrimps sampled in the Atlantic seeps and vents based on the ML analysis of partial mitochondrial COI sequence data using the GTR + Γ evolutionary model.

Unbiased heterozygosity (H_E) varied between 0.59 (West Africa) and 0.65 (Logatchev), and the observed heterozygosity (H_O) varied between 0.52 (Gulf of Mexico) and 0.62 (Logatchev). The tests for Hardy–Weinberg equilibrium revealed heterozygote deficiency, after correction for multiple tests for both seep sites (Table 4) except for the Logatchev vent, which showed no significant departure from equilibrium. Significant F_{IS} values were comprised between 0.09 and 0.18 and were homogeneous across loci.

Demographic analyses suggested the occurrence of population expansions, and these were significant for all studied sites when analysing mitochondrial data, with significant negative values for Tajima's D and Fu's F_S (Table 3), while with microsatellite data (bottleneck tests), only the West African cold seep population revealed a significant signature of population expansion (for all mutation models tested), as the expected heterozygosity estimated from allele frequencies (H_E) was significantly lower than estimates based on the number of alleles and sample size (H_{Eq}) ($P < 0.02$).

Pairwise comparisons between populations from the Gulf of Mexico seeps and the other two regions (Logatchev vent and West Africa seeps) revealed no differentiation (pairwise F_{ST} for COI haplotypes not significantly different from zero; $P > 0.05$) (Table 5). However, they were significant ($P < 0.05$) between the West Africa seeps and the Logatchev vent (Table 5). The pairwise F_{ST} estimates based on microsatellite loci revealed a similar pattern although with low but significant values between the West Africa seeps and the two other sites (Gulf of Mexico and Logatchev vent), after q-value correction for multiple tests (Table 5). Accordingly, the results from the Bayesian analysis performed with MIGRATE (Table 6) supported, consistently across the independent runs, the occurrence of high gene flow from the Logatchev vent to the Gulf of Mexico seeps.

For the ESU 2 clade, only *C. chacei* had sufficient sampling size for a population analysis. The pairwise F_{ST} estimate based on COI, between the two MAR vent locations, was very low and not significant (F_{ST} = 0.00017; $P > 0.05$).

Discussion

The results reported here reveal large-scale connectivity across distinct and patchily distributed chemosynthetic

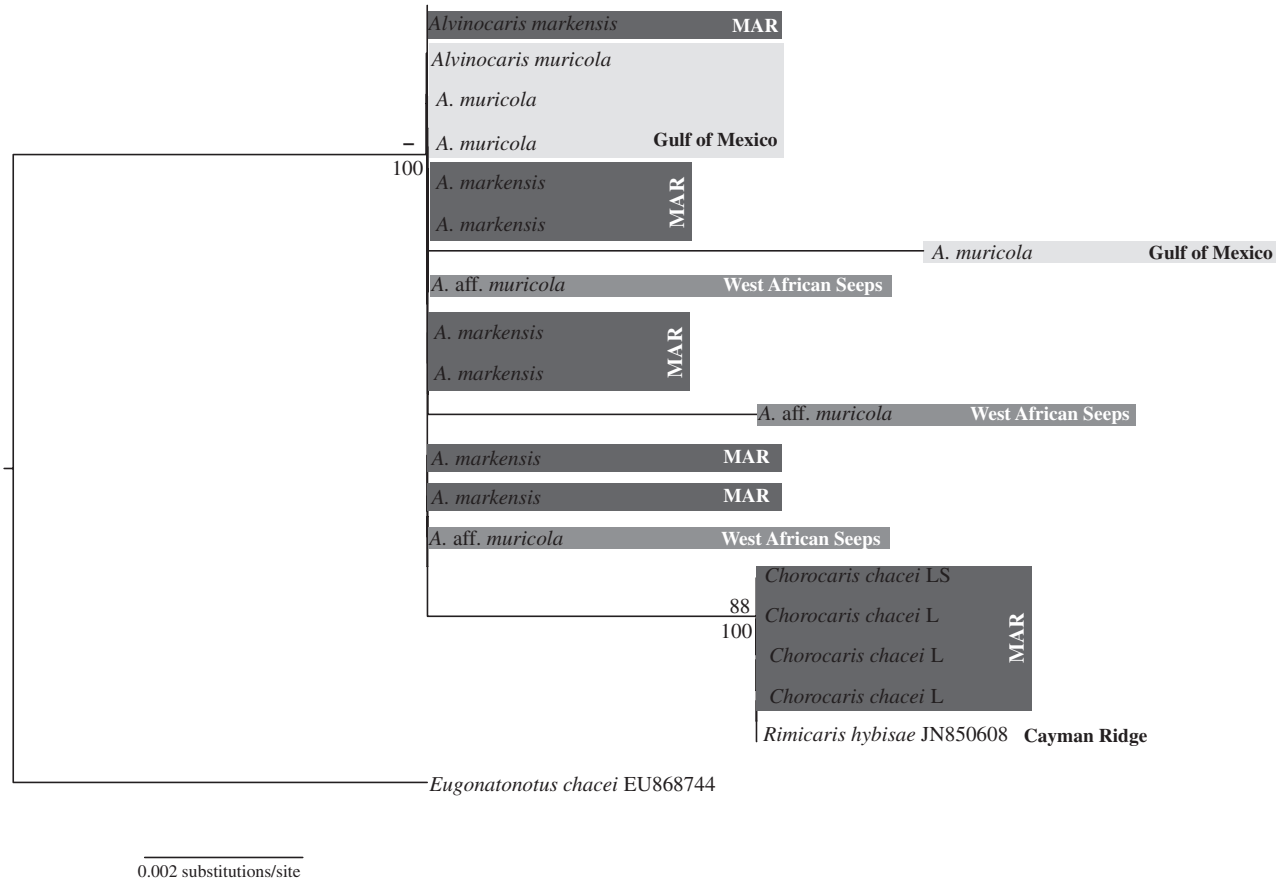

Fig. 4 Phylogenetic relationships of Alvinocarididae shrimps sampled in the Atlantic seeps and vents based on the ML analysis of partial sequences of the 18S ribosomal gene using the JC evolutionary model.

ecosystems. This supports the existence of efficient mechanisms facilitating dispersal and localization of suitable habitats. These findings also raise questions regarding the accuracy of endemism estimates, given our limited knowledge of ecosystems and communities distributed on the bottom of the oceans. We provide evidence for the occurrence of synonymous species for three of the taxa analysed in this study, one Vesicomyidae bivalve and two Alvinocarididae shrimp taxa, shared between hydrothermal vents and cold seeps across the entire AEB. This effect creates biases in the evaluation of community composition, diversity and connectivity across deep-sea ecosystems. The description of the same taxa or genetic entities under distinct species and genus names also prevents analyses of dispersal levels and directions across the entire distribution of the taxon or meta-population.

Vesicomyidae bivalve connectivity

The molecular characterization of the vesicomyid *A. southwardae* assigned to *Calyptogena* sp. was first conducted on specimens from the Western Atlantic seeps of Barbados and the Florida Trench (Peek & Gustafson 1997), and later found to be similar to specimens from the MAR Logatchev vents (Peek *et al.* 2000). Its morphological description (Krylova *et al.* 2010) also included specimens from the Vema fracture zone and empty valves from the Henry seamount, located close to the Canary Islands at 3500 m depth. Further molecular studies report this species at recently discovered sites in the South MAR hydrothermal vents (Stewart *et al.* 2008; Van der Heijden *et al.* 2012). Our study is the first record of this species from the Eastern Atlantic African cold seeps. Although no shared haplotypes were observed between regions, the few sequences available from GenBank for the Mid- and Western Atlantic are evolutionarily close to those reported here from African seeps, indicating that this might be the same species across all the AEB. Only one of the *A. southwardae* from the Barbados seeps was slightly more distant but still exhibited relatively low genetic divergence from the others (less than 1.2%, the maximum divergence level found among the sequences

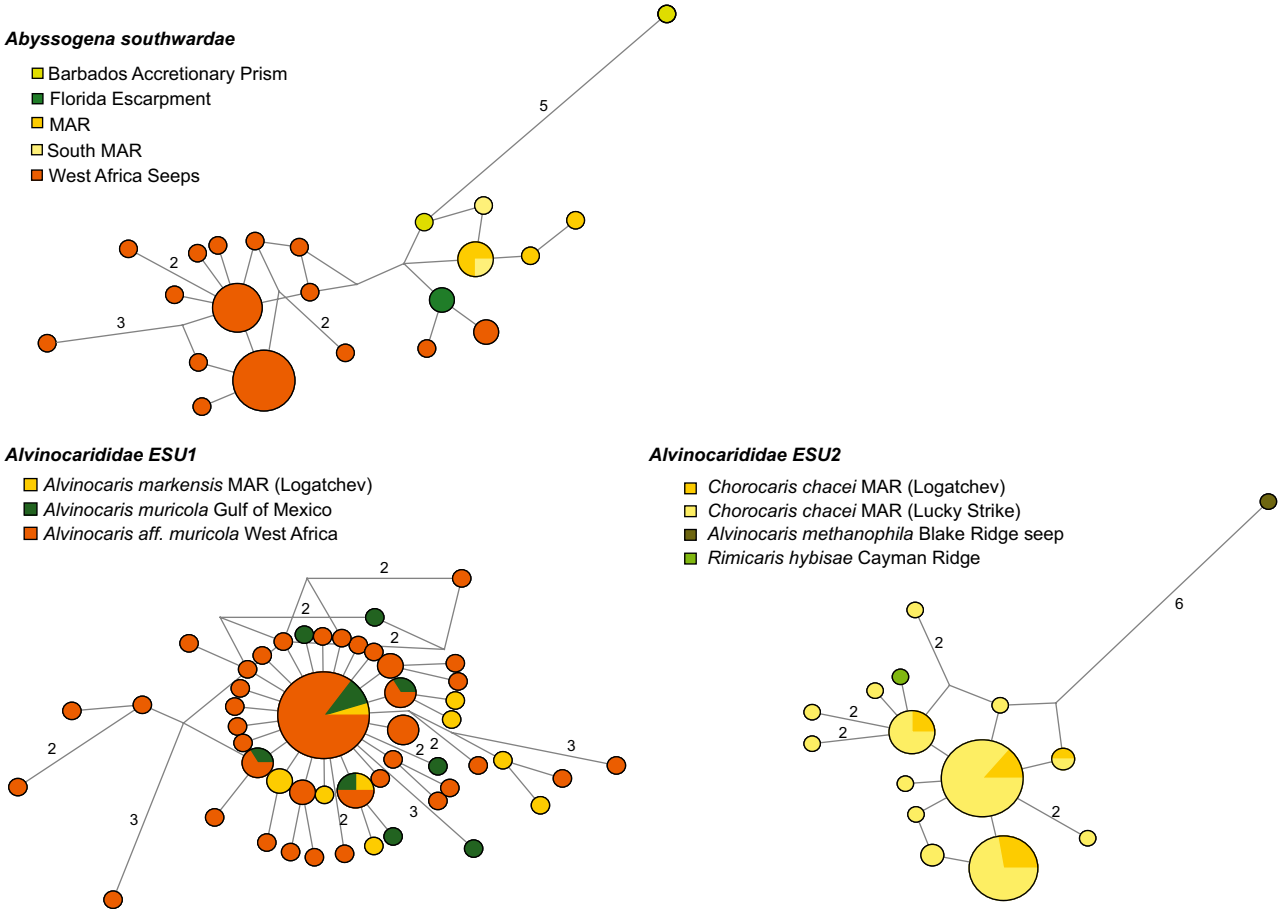

Fig. 5 Haplotype networks of the mtDNA haplotypes obtained for *Abyssogena southwardae* bivalves and for both clades (ESU1 and 2) recovered for the Alvinocarididae shrimp of the AEB. Each circle represents a different haplotype, with the size of each circle proportional to the number of individuals displaying that particular haplotype. The colours used represent the locations where the haplotypes were found and within pie charts, the segment size is proportional to the relative frequency of a haplotype in each population where it is present. Mutation steps are represented only when higher than 1.

Table 3 Genetic diversity indices based on COI partial sequences (517 bp) of the deep-sea shrimp *Alvinocaris* sampled across the Atlantic equatorial belt calculated for each sampled site

Site	*n*	*k*	*N*h	*N*ph	*h*	π_1	π_2	*D*	F_S
Gulf of Mexico	12	14	9	5	0.91 ± 0.08	2.47	0.0047	−1.99	−4.83
Logatchev	11	11	9	7	0.96 ± 0.05	2.87	0.0050	−1.01	−4.83
West Africa	78	43	37	33	0.80 ± 0.05	1.95	0.0037	−2.51	−27.45

(*n*) sample size; (*k*) number of polymorphic sites; (*N*h) number of haplotypes; (*N*ph) number of private haplotypes, that is, the number of haplotypes exclusive of a population; (*h*) haplotype diversity; (π_1) mean number of pairwise differences; (π_2) nucleotide diversity. Neutrality and population expansion tests: *D*, Tajima's *D*-test; F_S, Fu's F_S test. All values obtained for the neutrality tests were significant at the 5% level.

analysed), suggesting that they might all belong to the same taxon. The analysis of more samples, especially from those regions poorly represented in GenBank, would help to elucidate whether there are unsampled shared haplotypes across the AEB, or whether, on the contrary, the low divergence levels reflect recent differentiation among those sites.

Even with the extremely low sampling sizes available, it was already possible to reveal a close relationship among all sites, suggesting large-scale connectivity

for this species across the Atlantic. Indeed, Vesicomyidae bivalves are distributed worldwide, and the genus *Abyssogena* in particular has representatives in at least two Oceans (Atlantic and Pacific; Krylova & Sahling 2010; Fig. 2). Other Vesicomyidae bivalve species shared across oceans are also genetically similar, with several species displaying a trans-Pacific or Indo-Pacific distribution (Kojima *et al.* 2004; Audzijonyte *et al.* 2012; Decker *et al.* 2012; Van der Heijden *et al.* 2012; Fig. 2). These results indicate extremely large-scale dispersal capacity. This might have been either followed by persistent connectivity or, if isolated, then the divergence was too recent to be detected on the basis of mitochondrial sequences alone.

Table 4 Descriptive statistics based on nine microsatellite loci for *Alvinocaris* shrimp from ESU1 from all sampled locations

Site	*n*	*A*	A_{rich}	H_E	H_O	F_{IS}
Gulf of Mexico	14	5.8	5.47	0.64	0.52	**0.18*****
Logatchev	17	5.4	4.67	0.65	0.62	0.04
West Africa	67	8.8	4.89	0.59	0.53	**0.09*****

Number of individuals sampled (n), mean number of alleles across loci (*A*), A_{rich} standardized allelic richness for a minimum of 12 individuals, observed (H_O) and expected (H_E) heterozygosities and heterozygote deficiency (F_{IS}).
Bold numbers indicate significant values $^{**}P < 0.001$ after *q*-value correction.

Table 5 Pairwise F_{ST} values based on haplotype (COI) and allele frequencies (nine microsatellite loci) for the ESU1 *Alvinocaris* species sampled across the Atlantic equatorial belt

	COI marker		Microsatellite markers	
Sites	Gulf of Mexico	Logatchev	Gulf of Mexico	Logatchev
Gulf of Mexico				
Logatchev	−0.005		0.022	
West Africa	0.047*	−0.007	0.041***	0.078***

Significant levels are indicated $^{*}P < 0.05$; $^{**}P < 0.001$.

Alvinocarididae shrimp connectivity

Our data on the Atlantic Alvinocarididae shrimp revealed two well-supported clades shared across the Atlantic, each composed by samples from seeps and vents. The first clade (ESU 1) comprised *A. muricola* from the Western and Eastern Atlantic seeps and *A. markensis* from the MAR vents. We show here that these are synonymous taxa, with shared mitochondrial haplotypes and identical microsatellite polymorphism across the entire AEB including vents and seeps. Perhaps more surprisingly, the second clade (ESU 2) comprised specimens from different genera (*C. chacei*, *R. hybisae and A. methanophila*). These showed very low genetic divergence at levels similar to divergence between individuals of the same species. We posit that these taxa belong to the same genus, possibly even the same species.

In the genus *Alvinocaris* of the AEB (ESU 1), the hypothesis of synonymous species with high connectivity between all geographical locations was further supported by the intermingled distribution of haplotypes originating from different regions in a starlike haplotype network, with extremely low and mostly nonsignificant differentiation for both mtDNA and microsatellite data. The lack of or very low genetic differentiation found between sites was not due to low genetic diversity, as the 101 *Alvinocaris* individuals from the three localities across the Atlantic had even higher genetic diversity, than the high levels revealed for the shrimp species *Rimicaris exoculata* of the MAR (Teixeira *et al.* 2011a, 2012). At most, low sampling sizes for the Western and Central Atlantic could have contributed to the nonrejection of the null hypothesis of panmixia. Yet levels of F_{ST} were so low, that even if increasing sampling size would make them significantly different from zero, they would still be very low levels of differentiation. These results, together with the lack of genetic differentiation also found in shrimp from clade ESU 2

Table 6 Estimation of *M* and θ generated in MIGRATE analysis of mtDNA sequences (COI) of the ESU1 *Alvinocaris* species sampled across the AEB

Sites	Gulf of Mexico θ = 0.09	Logatchev θ = 0.0154	West Africa θ = 0.034
Gulf of Mexico	—	4.1×10^{-6} (3.1×10^{-6}–0.01)	1.4×10^{-5} (1.1×10^{-5}–0.04)
Logatchev	2×10^{3} (1.1×10^{3}–3.5×10^{3})	—	3.1×10^{3} (2.4×10^{3}–4.8×10^{3})
West Africa	3.7×10^{-5} (2.8×10^{-5}–0.09)	4.1×10^{-6} (3.1×10^{-6}–0.01)	—

Values in parentheses denote the 95% profile likelihoods for each estimate; all values were obtained in one independent run.
Donor populations represent the lines, and recipient populations represent the columns.

of the MAR vents, support the occurrence of large-scale effective migration across the Atlantic Ocean.

Demographic effects

For a species to persist as a single genetic entity over a large geographical range in a patchy habitat, gene flow between the separated populations must be high enough to compensate the differentiation originated by random genetic drift within isolated sites. However, a similar signature of low genetic differentiation may also arise when populations have a recent common origin (typical of recently colonized novel habitats; e.g. Neiva *et al.* 2012) and/or exhibit high effective population sizes limiting the effect of drift and resulting in incomplete lineage sorting despite a lack of connectivity.

Both Vesicomyidae bivalves and Alvinocarididae shrimp have been reported to display large population densities (>1000 individuals/m^2; Copley *et al.* 1997; Tyler & Young 1999). In the absence of temporal fluctuation or significant variance in reproductive success, high population densities might reflect large effective population sizes. However, the starlike topology of our haplotype network of the *Alvinocaris* shrimp together with the neutrality and bottleneck tests suggests a recent small effective population size followed by expansion. Such events cause instantaneous drift in each independent population, which would generate differentiation among populations, unless counteracted by connectivity. The joint observation of large-scale homogeneity and signatures of recent demographic events invalidates the hypothesis of large effective population size hiding ongoing divergence. Instead, it supports the hypothesis that contemporary high connectivity across the Atlantic seeps and vents is the most likely explanation for the results reported here.

More taxa should be investigated in the future to further test for the role of MAR as a significant stepping stone between Atlantic seep communities. Our results confirm the role of Mid-Atlantic vents as a stepping stone for at least the two taxa that had sufficient sampling to allow the test of this hypothesis, among the 72 reported thus far from Atlantic seeps (Olu *et al.* 2010). Additionally, our results highlight that the possible large-scale overall connectivity picture might be obscured by the suggested occurrence of synonymous species. In particular, distinct species (and sometimes genus) names discourage genetic studies to address connectivity. Indeed, recently an identical mitochondrial background was revealed among three distinct morphologically described species of tubeworms, *Escarpia* sp., from seeps along the Atlantic and the Eastern Pacific. This finding triggered population genetic studies that revealed large-scale dispersal at regional scales (Cowart *et al.*, 2013).

Connectivity

Many factors play a role in effective dispersal, such as fecundity, size of the source population, timing of reproduction, type of larval development, mortality and oceanic currents (Scheltema 1986). Large-scale dispersal has been inferred for many vent organisms regardless of their differences in early life history traits (see review Vrijenhoek 2010) that could influence dispersal ability, suggesting that these are poor predictors of effective dispersal. Indeed, *A. southwardae* and *Alvinocaris* spp. share a wide distribution and patterns of contemporary gene flow across the Atlantic, yet exhibit strikingly distinct larval development.

The reproductive biology of Vesicomyidae bivalves is poorly studied and undescribed for *Abyssogena* species. However, earlier studies showed that vesicomyid oocytes are usually ~200 μm in diameter, possibly supporting a lecitotrophic development (Lisin *et al.* 1997; Tyler & Young 1999; Parra *et al.* 2009). Lecitotrophs are generally assumed to be poor dispersers, but they can have very long pelagic residence times (Shilling & Manahan 1994) and eggs with a greater amount of yolk. Higher reserves may even represent an advantage by providing nourishment during long-distance dispersal across inhospitable habitats. But to date, no data are available regarding the larval dispersal capacities of Vesicomyidae bivalves.

Alvinocarididae shrimp have been mostly shown to exhibit planktonic larval development with relatively low fecundity (~400 eggs per female). The scarce information available suggests that the development could take place at shallower depths (Pond *et al.* 2000). For the species *Rimicaris exoculata*, it has been hypothesized that females release their eggs into vent plumes before hatching, as plankton samples at Broken Spur vent field contained eggs, which represented 95% of the biomass (Tyler & Young 1999). Also in the Atlantic, larval stages of *Alvinocaris* sp. and *Chorocaris* sp. have been captured in trawls at mid-water depths and at great distances from known vents (Herring & Dixon 1998). All available data therefore seem to support dispersal potential in the three dimensions of the Atlantic water masses, for at least these Alvinocarididae shrimp species.

Across the AEB the longitudinal flow of the North Atlantic Deep Water, enhanced by equatorial intermediate jets could theoretically provide a connection pathway along the Equator (Arhan *et al.* 1998). However, these deep currents have very low velocities, and the time taken to cross the Atlantic may represent a few years. These low velocities may at least in part be

compensated by their low temperatures that should slow down larval development, and delay metamorphosis (O'Connor *et al.* 2007). Besides, warmer and faster surface currents could offer enhanced crossing speed, on the order of few months (Olu *et al.* 2010). A study on dispersal of deep-sea larvae (Young *et al.* 2012) among seep communities along the Atlantic American margins indeed showed that shallow dispersal provided greater travelled distances for some of the species analysed. This study further supported that the eastward drift in the North Atlantic is unlikely to carry larvae from North America seeps to Western Africa. The authors suggested that if there is genetic exchange across the Atlantic, it is most likely unidirectional, from East to West in the Equatorial current system (Young *et al.* 2012). Accordingly our Bayesian analysis (MIGRATE) of mitochondrial data from *Alvinocaris* seems to consistently support a westward migration from the MAR to seeps in the Gulf of Mexico. As deep-sea shrimp have been reported as possibly having an ontogenetic vertical migration (Herring & Dixon 1998), they may take advantage of the faster shallow currents across the Equator.

A wide range of biological mechanisms and oceanographic pathways therefore exist that may facilitate, speed up or lengthen the duration of dispersal, and contribute to explain the large-scale dispersal of larvae across the Atlantic deep-sea ecosystems. Yet in a three dimensional ocean, considering the extremely fragmented distribution of vents and seeps, the probability of an individual reaching a suitable chemosynthetic habitat after being diluted in an incommensurable volume of water seems infinitesimal. The existence of dispersal mechanisms such as those delaying metamorphosis (as found for an alvinellid polychaete, Pradillon *et al.* 2005), or actively guiding larvae (or adults in cases where they are significantly mobile) towards suitable habitat, or through vertical migrations that catch more favourable currents, seems a more parsimonious additional explanation. Indeed, deep-sea larvae can potentially move into water of different temperatures and in some cases different pressures; this may lead to alterations in metabolism, feeding rate and other vital processes (Young *et al.* 1996, 1998), extending pelagic larval durations (PLD) (O'Connor *et al.* 2007). A hypothesis of active directed migration could involve the detection of stimuli such as water chemistry, sound, polarized light, current direction, magnetism and water pressure, as found for other organisms (Kingsford *et al.* 2002), or a combination of such mechanisms with extremely delayed larval development linked to low temperatures in the deep-sea (O'Connor *et al.* 2007).

Another nonexclusive hypothesis to explain high connectivity is the possible occurrence of more stepping-stone habitats than acknowledged. Additional favourable habitats may exist that might have remained undetected thus far due to an extremely low mapping and exploration effort, although extremely valuable. This might cause an erroneous appraisal of deep-sea species ranges, endemicity and connectivity (Audzijonyte & Vrijenhoek 2010) due to very low, spatially scattered and ecosystem-biased, sampling coverage. Indeed, Samadi *et al.* (2006) showed that high endemism previously reported for some Pacific seamounts was for a large number of taxa an artefactual observation due to low sampling densities focused on a limited geographical area. By increasing sampling pressure at larger geographical scales, these authors demonstrated that most presumed endemic species were also found in other habitats, leading them to propose that seamounts are biodiversity rather than endemism hot spots.

Exploration of deep-sea habitats is very biased towards seamounts, active vents and seeps, because these oases of life can be detected from the surface due to the geological anomalies with which they are associated. The present-day knowledge of the distribution of reducing environments in the whole deep-sea is largely underestimated (Audzyjonite & Vrijenhoek 2010). However, whale- and wood-falls encountered by chance harboured chemosynthetic communities similar to those observed at seeps and vents. These temporary ecosystems may act as stepping stones (Black *et al.* 1997) dispersed across the seabed ensuring connectivity among chemosynthetic ecosystems. Indeed, several species of Vesicomyidae bivalves have been, for example, described from deep-sea expeditions of the early 20th century (e.g. Valdivia, Thiele & Jaeckel 1931) without description of their biotope (Cosel & Olu 2009), and occasionally these old records are identified as the same species as those from cold seeps (e.g. *Christineconcha regab* from the Bay of Biscay and the Regab pockmark; Krylova & Cosel 2011). Incidentally, on an artificial wood deployment about 300 m away from any active site near Logatchev (MAR), *Alvinocaris* shrimp were observed but unfortunately not collected (S. Hourdez, personal observation). The large-scale dispersal observed in previous studies and confirmed here across the whole Atlantic Ocean raises the question of how many suitable habitats not associated with *easily* detectable geological anomalies might remain to be discovered in the depths of the oceans in order to gain a global picture of deep-sea biodiversity and biogeography.

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K.O., C.D., S.H. and S. A. collected the field data. S.T, C.D. and S.F. obtained the genetic data. S.T, C.D. and R.L.C. analysed the data. E.A.S. and S.A. contributed with reagents/materials/analysis tools. S.T. and S.A. conceived the ideas. S.T., E.A.S. and S.A. interpreted the data and wrote the article. All authors critically revised the manuscript.

Data accessibility

DNA sequences GenBank accessions: *Abyssogena southwardae* COI haplotypes: \JX900981—\JX901014; Alvinocarididae shrimp COI haplotypes: \KC840879—\KC840940; Alvinocarididae shrimp 18S rRNA haplotypes: \KC840876—\KC840878.

Aligned sequences and microsatellite genotypic data: Dryad doi: \10.5061/dryad.cv910.