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Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the Azores plateau

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Abstract

Near the Azores Triple Junction as the Azores Plateau is approached, the ridge axis becomes shallower; its depth decreases from ca. 2400 m in the RAINBOW vent field (36°13'N) to ca. 850 m in the MENEZ GWEN vent field (37°35'N). In this area, extensive mussel beds of the mytilid *Bathymodiolus azoricus* dominate the hydrothermal vent fauna, along with populations of three shrimps (*Rimicaris exoculata*, *Mirocaris fortunata* and *Chorocaris chacei*). The main physical and chemical characteristics of the vent habitat were studied by discrete sampling, in situ analysis and sediment trap moorings. The vent fauna is distributed along a variable band where the vent fluids and seawater mix, with *R. exoculata* living in the most concentrated areas and *Bathymodiolus azoricus* in the most diluted zones. Various non-endemic species live at the border of the vent field. The variations observed in structure and composition of the communities along the depth gradient are most likely due to changes in vent fluid toxicity (metallic and sulphide content) and suspended mineral particles, which render the fluids harsher for species living there. The main faunal differences observed between LUCKY STRIKE and MENEZ GWEN hydrothermal fields are due to an impoverishment in the hydrothermal endemic species and to the penetration of bathyal species. The comparison of the three studied vent fields suggests the existence of a succession of several biogeographic islands rather than a single province. © 2001 Published by Elsevier Science Ltd.

Keywords: Deep-sea; Hydrothermal vents; Mid-Atlantic Ridge; Azores Triple Junction; Ecosystems; Habitat characterisation

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1. Introduction

The discovery of hydrothermal vents on ocean ridge crests occurred in 1977, off the Galapagos Islands (Lonsdale, 1977), but the exploration of the mid-Atlantic Ridge only started in 1985 (see Van Dover (1995) for details). Several ecological studies (Segonzac, 1992; Van Dover, *o.c.*) on the two main deep hydrothermal vent fields, TAG (26°N) and Snake Pit (23°N) ca. 3500 m deep, showed faunal assemblages very different from those found on the East Pacific Rise. Caridean shrimps, in particular *Rimicaris exoculata*, dominate populations in these deep Atlantic fields. Conversely, alvinellids and tube-worms are not observed.

In 1992, during the US mission FAZAR, a new site was discovered at 37°18'N, 1700 m deep (LUCKY STRIKE). A preliminary study of the communities' composition at this site was done during six dives of the US deep research submersible ALVIN¹ and suggested the existence of two distinct biogeographical provinces on the Mid-Atlantic Ridge (Van Dover et al., 1993). Following the first discovery, the European Union programme MAST 2 — MARFLUX/ATJ,² the diving cruises³ of the French submersible NAUTILE, the MAST 3 AMORES⁴ programme and the Portuguese-French SALDANHA⁵ cruise, continued and completed the exploration of the Azores Triple Junction area, establishing its depth limits. From 1993 to 1998, the hydrothermal vent communities thriving in three major vent fields located on three segments of the southeastern limb of the Azores Triple Junction (RAINBOW, LUCKY STRIKE and MENEZ GWEN) within 2° of latitude, were explored and studied.

The deep-sea hydrothermal vent community composition and structure are affected (1) by linking and isolating mechanisms between vent fields (Hessler and Lonsdale, 1991; Tunnicliffe, 1991), (2) by local conditions (chemistry and particle content of fluids and substratum patterns) (Johnson et al., 1988), and (3) by instability of venting, which induces an extinction-colonization dynamics (Cann et al., 1994; Desbruyères, 1998; Chevaldonné et al., 1997). In the Azores Triple Junction area, as the Azores Plateau is approached, the ridge axis gets shallower; its depth decreases from ca. 2400 m in the RAINBOW vent field (36°13'N) to ca. 850 m in the MENEZ GWEN vent field (37°35'N). Because of phase separation processes, the accompanying drop in hydrostatic pressure directly affects the chemistry of the high-temperature effluents and their mineral particle content. Source rocks hosting the hydrothermal convection also affect the chemistry of the effluents and deposits. The RAINBOW ultramafic hosted system produces acidic fluids enriched in metals and gases (H₂ and CH₄) and relatively impoverished in H₂S (Charlou et al., 1997). The physical settings of the area studied provide a unique opportunity to describe the influence of a wide range of chemical and physical factors on the composition, distribution and dynamics of vent communities at slow spreading ridges when geographical isolation by transform faults is absent or reduced.

¹ Lucky Strike Cruise, May–June 1993, Chief-Scientist, Charles Langmuir.

² Coordinator Henry Bougault, IFREMER, France.

³ DIVA 1 Cruise, May 1994, Chief-Scientist Yves Fouquet and DIVA 2 Cruise, June–July 1994, Chief-Scientists Daniel Desbruyères and Anne-Marie Alayse.

⁴ FLORES Cruise, July–August 1997, Chief-Scientist Yves Fouquet; MARVEL Cruise, August–September 1997, Chief-Scientists Daniel Desbruyères and Anne-Marie Alayse and PICO Cruise, June–July 1998, Chief Scientist and Programme Coordinator, Daniel Desbruyères.

⁵ July 1998, Chief-Scientist Fernando Barriga.

2. Materials and methods

2.1. Animal collection, mapping and microdistribution

The present study is based on in situ observation with the submersible NAUTILE, video record analyses and fauna sampling during dives. Data are provided by four cruises, in summer 1994 (DIVA2), 1997 (MARVEL) and 1998 (PICO & Victor Première). Mapping of vent sites was done with NAUTILE's acoustic navigation records on high-resolution EM12 bathymetric maps (from FLORES cruise), and the GIS analysis ArcView® software. At selected hydrothermal sites, video analysis was used to describe the microdistribution of each species and its relationship with substratum and fluid escaping structures.

2.2. Chemical and thermal characterisation of the habitats

Fluid samples were obtained with two samplers manipulated by the submersible NAUTILE: 750 ml titanium syringes (Von Damm et al., 1983) associated with an autonomous temperature probe for the hot fluids and a new multisampler unit using four 200 ml titanium bottles associated with an autonomous temperature probe. Sampling was done between and inside the populations marked with quadrats 0.5×0.5 m in size as topographic benchmarks. Water sampling locations were chosen in relation to faunal assemblages and microenvironments: (1) fluid diffusion or vent proximity, (2) within *R. exoculata* swarms, (3) inside *Mirocaris fortunata* populations, (4) on mussel-beds (small- or large-sized) and (5) associated or not with shrimps (*M. fortunata* and *Chorocaris chacei*).

During the “VICTOR PREMIÈRE” cruise, a new chemical analyser (Le Bris et al., 2000) was successfully tested in the LUCKY STRIKE area, and a series of in situ ΣS (total dissolved sulphide), nitrate and temperature data were obtained. This in situ analyser, called ALCHIMIST, is based on flow injection analysis and colorimetric detection. Sample processing and analytical methods are displayed in Table 1.

Discrete temperature measurements were made with the probe operated by the submersible, and temperatures over a time series were obtained at different population beds with HOBO® and MICREL® probes (Fornari et al., 1994). Calibration was done with a standard reversing thermometer.

2.3. Particulate fluxes

At MENEZ GWEN and RAINBOW (“Flores 5” vent) vent fields, triple sediment traps (see Khripounoff and Albéric (1991) for description) were deployed by the submersible NAUTILE during the MARVEL cruise for 10 and 16 days, respectively. On both occasions the trap was set close to an active vent. At LUCKY STRIKE vent field, a triple trap was deployed 1.5 m south of a smoker called SINTRA during the DIVA 2 cruise. In order to obtain a pelagic flux reference, another triple trap was also moored during the MARVEL cruise outside MENEZ GWEN hydrothermal field. Prior to deployment, the sampling bottles were filled with filtered seawater. No poison was added because bacterial decomposition was considered to be negligible during the mooring time (2×5 days at MENEZ GWEN, 4×4 days at RAINBOW and 1×25 days at LUCKY STRIKE. After recovery, samples were

Table 1

Sample treatment and analytical methods used in the study of microenvironments

Parameter	Processing	Analytical method	Remarks
pH	Analysis on board	Potentiometry electrode for sulphide-rich medium	25°C TRIS buffer
ΣS ($H_2S + HS^-$)	Analysis on board	Colorimetry (Fonselius, 1983)	DL ^a = 0.5 $\mu\text{mol l}^{-1}$ rsd = 5%
ΣCO_2 , CH_4	Analysis on board	Head space-GC-HWD FID (Sarradin and Caprais, 1996)	10%
Nutrients ^b	Freezing	Colorimetry, segmented flow	rsd = 5%
Cu, Pb total dissolvable metal	HNO_3 suprapur®, 20 μl in 20 ml, ambient T	Potentiometric stripping analysis (Riso et al., 1997)	Cu rsd = 5% Pb rsd = 5%
ΣS and $NO_3^- + NO_2^-$	In situ analysis ALCHIMIST	FIA (Le Bris et al., 2000)	1.5%

^aDL = detection limit.^b NH_4^+ , $NO_3^- + NO_2^-$.

stored in the dark at 4°C pending analyses. In the laboratory, macro- and meio-organisms were removed from the particle samples. Samples were then rinsed with Milli-Q purified freshwater (pH ~ 7), freeze-dried and weighed. Total carbon and nitrogen contents were measured in duplicate with a Carlo-Erba® NA 1500 auto-analyser. Organic carbon content was measured with a Leco® WR12 elemental analyser after removal of carbonates with a 2 N HCl solution (Weliky et al., 1983). Inorganic carbon content was calculated as the difference between total and organic carbon contents. Total sulphur was determined with a Leco® CS-125 auto-analyser. Elemental analysis of particles was undertaken by EDAX® 1 DX-4i X-ray spectrometry. Standards were prepared in the laboratory from pure chemical compounds. The average accuracy of the analyses was 15%.

3. Results

3.1. Physical settings and faunal characteristics

From north to south, three distinct vent fields were visited (Fig. 1).

MENEZ GWEN is situated in the volcanic segment between 37°35'N and 38°N. The main system is formed by a 700 m high volcano, 17 km in diameter (Fouquet et al., 2000). A 2 km wide axial graben splits its summit. Several active sites were located on the southeast and east slopes of one small volcano growing at the northern end of the bottom of the graben (Fig. 2) at depths ranging from 840 to 865 m. At "PP 10/F 11" sites hydrothermal precipitates cover an area of about 50 m in diameter. Anhydrite chimneys up to 2 m high are present at the summit of this low elevated hydrothermal mound. A few patches (500 cm² each) of mussels were present. A few geryonid crabs (*Chaceon affinis*) were present in the vicinity. A second and more important site (markers D 9, PP

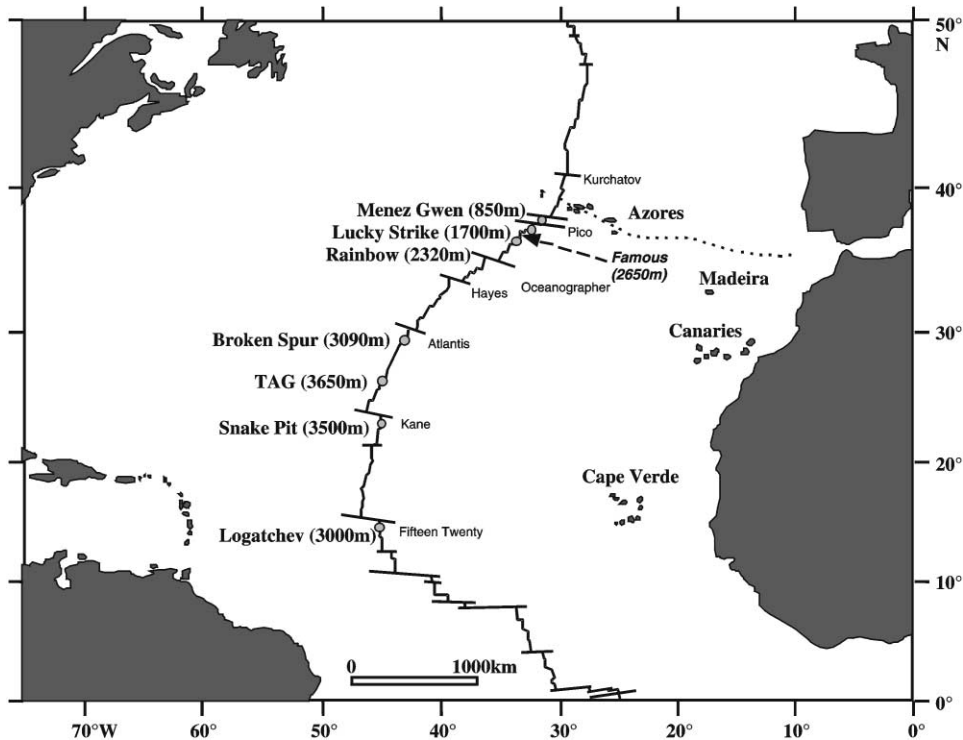


Fig. 1. General location map of the eight active hydrothermal vent fields known to date on the Mid-Atlantic Ridge between Equator and the Azores Archipelago. The major transform faults, which constitute the principal isolation structures, are also drawn on the map.

11, F 12) is located in an escarpment on the slope, between 860 and 842 m depth. It is bordered in the upper part by a field of pillow lava and laterally by crumbled rocks. Hydrothermal deposits, from which a 10–40°C refringent fluid diffuses, occupy the centre of the site. An active chimney situated on the northwest escarpment belched out fluid at 277°C. The site's periphery was occupied by a little dense belt of hydroids. Numerous bathyal fishes have been found around the site: *Chaunax* sp., *Trachyscorpia cristulata echinata*, *Neocyttus helgae*, *Epigonus telescopus* and *Beryx splendens* (Saldanha and Biscoito, 1997). In the limit between lava and the anhydrite deposits, there were important mussel colonies. Specimens sampled showed a maximum shell length of 111 mm. There were no commensal scale-worms inside these mussels. Numerous patelliform gastropods were present on the mussels' shells, in particular *Protolira valvatooides* and one new species of the genus *Lepetodrilus*. These mytilid populations consisted mainly of large individuals ($l > 40$ mm), but the two younger cohorts (modes 4 and 18 mm) were also present and represented ca. 20% of the population (Comtet and Desbruyères, 1998). Extensive bacterial mats covered some of these populations. On the active deposits (chimney walls) and amongst mussels, important populations of *C. chacei* and *M. fortunata* were found. *S. mesatlantica* was the dominant indigenous predator, while many *C. affinis* came to feed on the mussels.

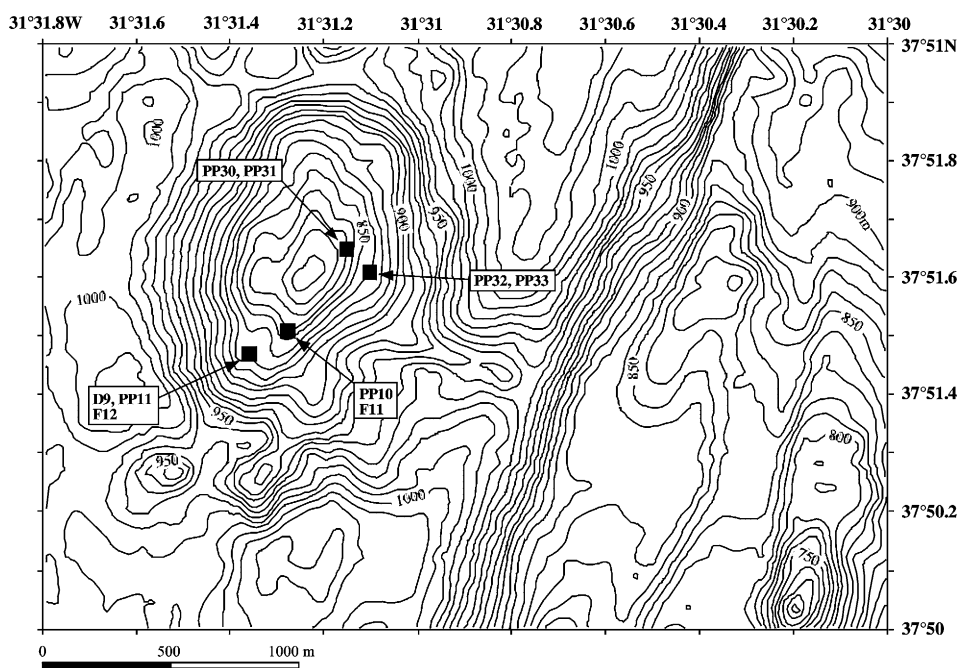


Fig. 2. Map of the MENEZ GWEN vent field ("EM 12" bathymetric survey — FLORES cruise). The small (young) volcano is growing on the bottom of the axial graben, which split an 800-m tall circular volcano situated at the centre of the volcanic segment adjacent to LUCKY STRIKE segment.

At the PP 32/33 markers, the faunal characteristics were similar to the above. Mussel populations were very important and covered virtually all-available rock surfaces. In contrast with previously studied sites, the size of mussels in this population was heterogeneous. Some mussels carried the commensal *Branchiopolynoe seepensis*. Numerous gastropods were present on the mussels. Geryonid population around and inside the site was important. A single fish of the genus *Gaidropsarus* was observed inside a crevice amongst mussels.

LUCKY STRIKE is one of the largest known active fields in the modern ocean. The hydrothermal fluid, with a temperature ranging between 170 and 324°C, has fluid characteristics (temperature, chlorinity and gas concentration) varying from site to site within the field (Charlou et al., 2000a,b). The hydrothermal vent sites of this field are distributed around a lava lake (Fig. 3), in particular in the southeastern and northwestern zones. Well-defined active chimneys such as Eiffel Tower, Y3 or Elizabeth, belching out very hot fluids and zones where hydrothermal activity is more diffuse can both be found at LUCKY STRIKE. For practical reasons, an equivalence of vent site names given during French and American cruises corresponding to passive markers is proposed (Table 2).

The fauna is described from the biggest and most studied site EIFFEL TOWER considered as example of the Lucky Strike field. In fact, no noticeable difference was observed in the dominant species composition or microdistribution except at the Y3 site. Except for the flaky anhydrite- and barite-clad steep slopes, which were inhabited by more or less extensive populations of *M. fortunata*, the edifice walls of EIFFEL TOWER were covered by *Bathymodiolus azoricus*. The Polynoidae

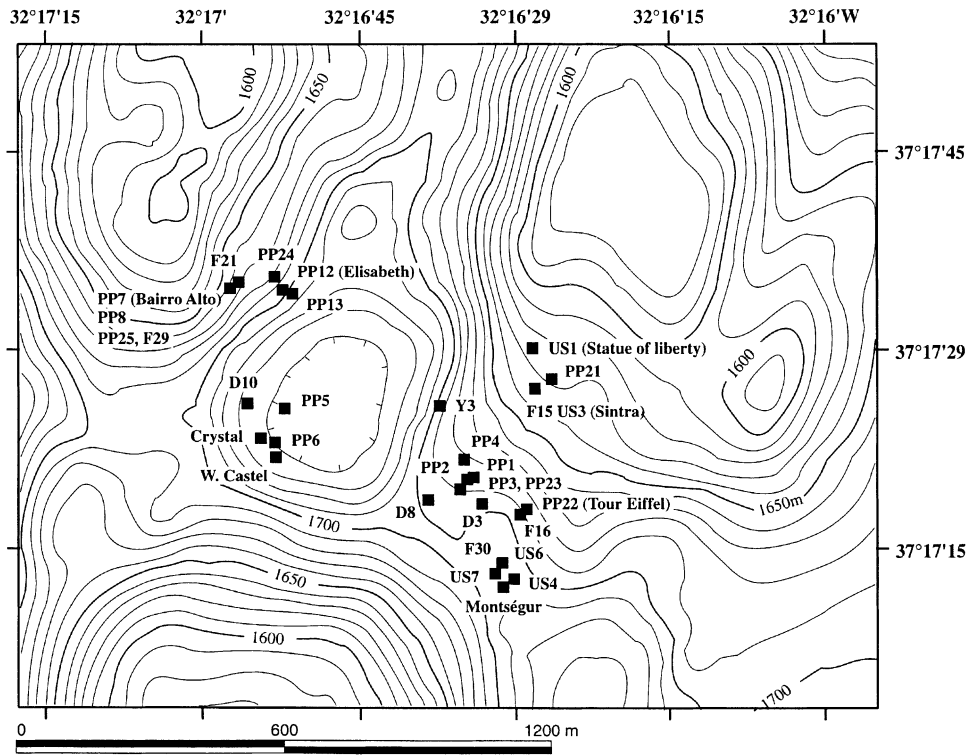


Fig. 3. Map of the LUCKY STRIKE vent field showing the location of the active sites ("EM 12" bathymetric survey — FLORES cruise). The central topographic high is made up of a composite volcano 13 km long, 7 km wide and 430 m high and divided into two parts separated by a N–S valley. The eastern part has a semicircular shape with three volcanic cones at its summit. The LUCKY STRIKE vent field is situated around a circular lava lake between these three cones.

B. seepensis was present in almost all mussels collected. Mussel distribution at EIFFEL TOWER was of particular note. A simple direct observation showed size segregation in the mussel beds (Comtet and Desbruyères, 1998; Comtet, 1998) within the same site. In the samples collected on isolated substrates (sulphide blocks and fragments) inside an active site, size spectrum analysis showed that small individuals colonised less active zones, whereas large individuals were found in active areas, on the smokers' walls, near the vent apertures. This is the reason why certain samples were dominated (75%) by individuals belonging to the first cohort (mode 4.35 mm) whilst in others 63% of the individuals belonged to older cohorts (modes 13–91 mm). Dense mats of filamentous bacteria covered certain areas of mussel beds of both sites. In the samples taken from mussel beds, several accompanying species were found, in particular gastropods belonging to genera *Protolira*, *Pelto-spira*, *Lepetodrilus* and *Shinkailepas* and the amphipod *Luckia striki*. On the walls of small active diffusers of low and medium temperature (30–90°C, e.g. in a small diffuser), several tens of very active individuals of *C. chacei* were observed. Numerous *S. mesatlantica* and pycnogonids were present on the mussel beds, a large proportion of which was covered by filamentous bacteria. Numerous shrimps, mostly juveniles of *M. fortunata* or *C. chacei*, were aggregated around flanges trapping hydrothermal fluid at the base of the edifice. *C. chacei* was also abundant among mussels.

Table 2

Equivalence between vent site names given during French and American cruises

Name	Markers PP	Markers Diva	Markers Florès	Markers US
Statue of Liberty				US1
Sintra	PP21		F15	US3
L'aiguille/M. Soares	PP4		F24	
Petit chimiste	PP1			
Fantôme	PP3–PP23			
	PP2			
Eiffel Tower	PP22	DII, IV, V, VI	F16	
Chimiste		DIII		
Isabel		DVIII	F22	US6
			F30	US7
				US4
Montségur				
Hélène	PP6		F17–F18	White Castel
Pico	PP5			Crystal vent
Nuno		DX	F19	
Bairro Alto (ex. Pagodes)	PP7–PP8 PP25		F29–F21	
Elisabeth	PP12–PP13			Jason
	PP24			
Y3		DI	F14	2608 site

In the crevices within the site perimeter, several filter-feeding species were observed in low densities, such as pedunculate cirripeds, as were small sessile carnivores such as *Candelabrum phrygium* (hydroid). There was an abundant bathyal ichthyofauna around the sites, which make frequent intrusions. The chimerid *Hydrolagus pallidus* was quite frequent; two or three individuals of *Cataetys laticeps* were always present at EIFFEL TOWER base as well as several *Gaidropsarus* n. sp. living at a smoker's base inside crevices of the edifice. *Lepidion schmidtii* was also frequently observed (Saldanha and Biscoito, 1997, 2000).

The Y3 site is distinguishable from other LUCKY STRIKE sites by the occurrence of *Rimicaris exoculata* in the upper and most active part of the edifice, mostly aggregated in crevices, when mussels are concentrated at the base of the structure.

The RAINBOW vent field (36°13'N) is situated in the north AMAR segment (Fig. 4). It is the deepest active segment of the ATJ area (2270–2320 m). The most active smokers are located at the western and eastern ends of the hydrothermal field. The west zone has the roughest relief, while the sites of the eastern zone are located on a sedimentary plateau. The highest developed sites are located at the field centre (PP 28/35 and PP 29/37) and are either active edifices or nearly “extinct” smokers. Hydrothermal sediments border the vent field.

The youngest and most active sites (e.g. East sites and West sites) in this field were nearly azoic, with the exception of the periphery of the western sites, where some sessile species were found. Hydroids formed fairly dense covers over the surrounding hard substrates. In the eastern region,

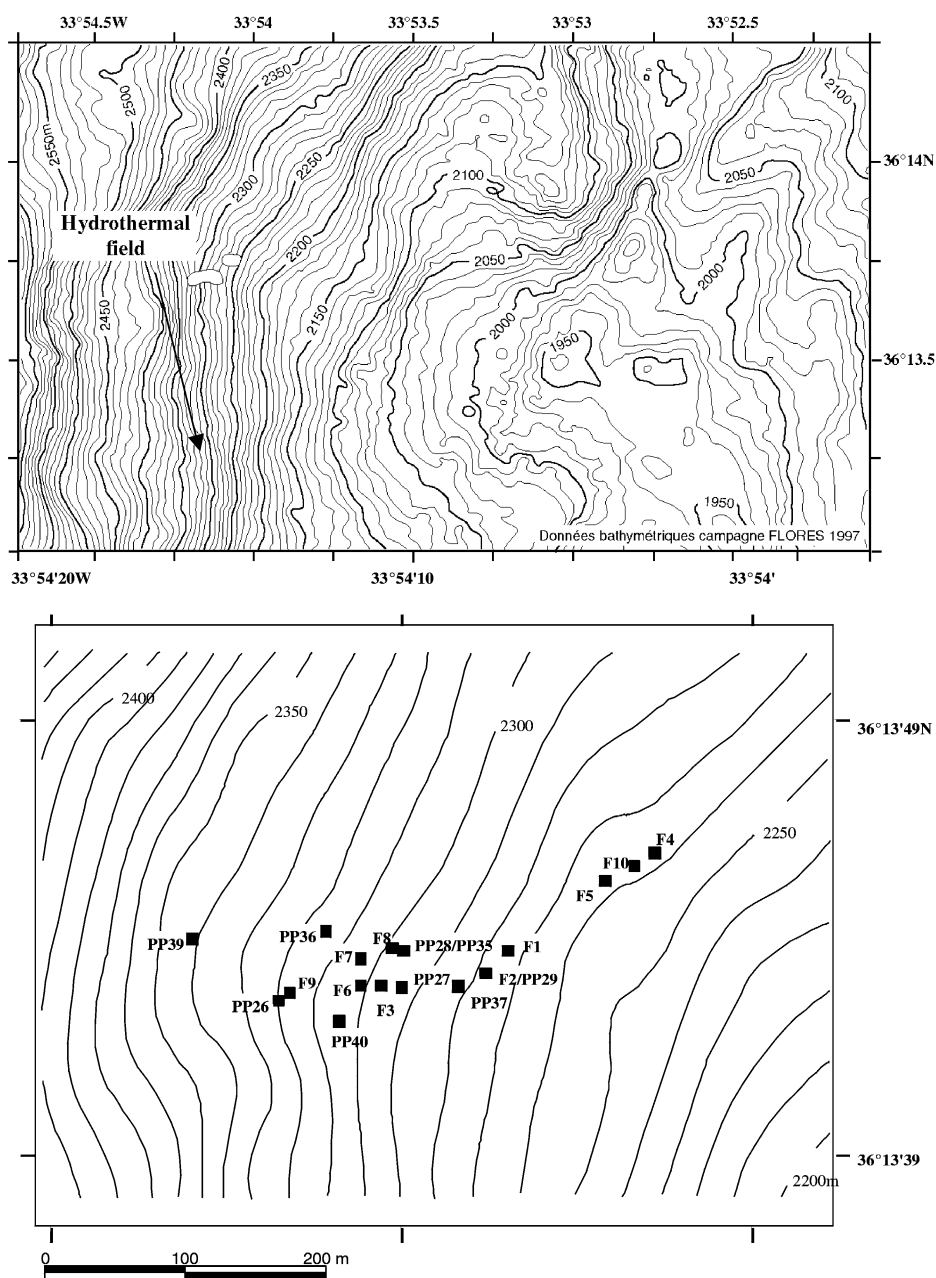


Fig. 4. Map of the RAINBOW vent field. Left, the distribution of active sites. Right, topography of the overall area (EM 12 bathymetric survey — FLORES cruise). The Rainbow vent field is situated on the Rainbow Ridge in the north of AMAR segment.

the polychaete *Spiochaetopterus* sp. formed dense and patchy populations inside hydrothermal sediments near the site. On the active crest to the west of the field, *M. fortunata* was observed in relatively dense aggregations along with some individuals of *R. exoculata* and *C. chacei*. No mussels

Table 3

Faunal composition of the vent communities at the three vent fields (MENEZ GWEN, LUCKY STRIKE and RAINBOW)

Phylum		Genus	Species	MG	LS	R	déterm.
Porifera	Hexactinellidae	<i>Asbestopluma</i>	<i>pennatulula</i>		*		Vacelet
		<i>Asbestopluma</i>	<i>infundibulum</i>		*		id
		<i>Cladorhiza</i>	aff. <i>grimaldi</i>		*		id
		<i>Euchelipluma</i>	<i>pristina</i>		*		id
Cnidaria	Anthozoa	<i>Stegolaria</i>	<i>geniculata</i>			*	Vervoort
	Hydrozoa	<i>Candelabrum</i>	<i>phrygium</i>		*		id
		<i>Eudendrium</i>	sp.		*		Marques
		<i>Eudendrium</i>	<i>rameum</i>			*	Marques
Annelida	Polychaeta	<i>Cladocarpus</i>	<i>formosus</i>			*	Vervoort
		<i>Amathys</i>	<i>lutzi</i>		*	*	Desbruyères
		<i>Archinome</i>	sp.			*	Kudenov
		<i>Branchiopolynoe</i>	aff. <i>seepensis</i>	*	*	*	id
		<i>Capitella</i>	sp.		*		
		<i>Eunice</i>	<i>norvegica</i>	*			id
		Cf. <i>Hesiolyra</i>	sp.		*		id
		<i>Levensteiniella</i>	n. sp.		*		Pettibone
		<i>Lugia</i>	sp.		*		Desbruyères
		<i>Opisthot-rochopodus</i>	n. sp.		*	*	Pettibone
		<i>Spiochaetopterus</i>	sp.			*	Petersen
		<i>Prionospio</i>	n. sp.1		*	*	Desbruyères
		(<i>Minuspio</i>)					
		<i>Prionospio</i>	sp.2		*	*	id
		(<i>Minuspio</i>)					
		<i>Prionospio</i>	sp.3		*		id
	Monoplacophora	<i>Rokopella</i>	n. sp.			*	Warén & Bouchet
Mollusca	Gastropoda	<i>Alvania</i>	n. sp.	*	*		id
		<i>Amphissa</i>	<i>acuticostata</i>	*			id
		<i>Calliostoma</i>	<i>obesula</i>	*			id
		<i>Dendronotus</i>	<i>comteti</i>		*		Valdes & Bouchet
		<i>Emarginula</i>	sp.	*			Warén & Bouchet
		<i>Laeviphritus</i>	n. sp.		*	*	id
		<i>Lepetodrilus</i>	n. sp.	*	*	*	id
		<i>Lirapex</i>	n. sp.		*		id
		<i>Mitrella</i>	<i>nitidunila</i>			*	id
		<i>Neusas</i>	<i>marshalli</i>	*			id
		<i>Orbitestella</i>	n. sp.		*		id
		<i>Orbitestellidae</i>	n. sp.	*	*	*	id
		n. gn.					
		<i>Paraletopsis</i>	n. sp.		*		id
		<i>Peltospira</i>	n. sp.		*		id
		<i>Phymorhynchus</i>	n. sp.		*		id
		<i>Protolira</i>	<i>valvatoides</i>	*	*	*	id
		<i>Protolira</i>	<i>thorvalldssoni</i>	*	*	*	Warén
		<i>Pseudorimula</i>	<i>midatlantica</i>		*		Warén & Bouchet
		<i>Pseudosetia</i>	<i>azorica</i>	*			id
		<i>Shinkailepas</i>	n. sp.	*	*	*	id
		<i>Strobiligera</i>	<i>brychia</i>	*			id
		<i>Xylodiscula</i>	n. sp.	*	*	*	id
Arthropoda	Bivalvia	<i>Bathymodiolus</i>	<i>azoricus</i>	*	*	*	Von Cosel, Comtet et al.
	Pycnogonida	<i>Sericosura</i>	<i>heteroscela</i>		*		Child & Segonzac
	Halacarida	<i>Halacarellus</i>	<i>alvinus</i>		*		Bartsch
		<i>Copidognathus</i>	<i>alvinus</i>		*		Bartsch

Table 3 (continued)

Phylum		Genus	Species	MG	LS	R	déterm.
Arthropoda	Cirripeda	<i>Altiverruca</i>	<i>longicarinata</i>			*	Young
		<i>Poecilasma</i>	<i>aurantia</i>	*			id
		<i>Poecilasma</i>	<i>crassa</i>	*			id
		<i>Verum</i>	n. sp.			*	id
	Copepoda	<i>Aphotopontius</i>	<i>atlanteus</i>	*	*		Humes & Segonzac
		<i>Aphotopontius</i>	<i>temperatus</i>		*		Humes
		<i>Stygiopontius</i>	<i>rimivagus</i>				Humes & Segonzac
	Ostracoda	<i>Bathyconchoecia</i>	<i>pauluda</i>	*	*		Carbonel
		<i>Bairdia</i>	sp.	*			id
		<i>Bythocypris</i>	sp.	*			id
		<i>Krithe</i>	sp.	*			id
	Amphipoda	? <i>Pontocypris</i>	sp.	*	*		id
		<i>Luckia</i>	<i>striki</i>		*		id
		<i>Bouvierella</i>	<i>curtimana</i>		*		id
		<i>Gitanopsis</i>	<i>alvina</i>		*		id
	Decapoda	<i>AcanthePHYra</i>	<i>eximia</i>		*		Biscoito
		<i>AcanthePHYra</i>	<i>purpurea</i>		*		id
		<i>Kemphyra</i>	sp.			*	id
		<i>Nematocarcinus</i>	<i>exilis</i>		*		id
		<i>Chaceon</i>	<i>affinis</i>	*			id
		<i>Paromola</i>	<i>cuvieri</i>	*			id
		<i>Segonzacia</i>	<i>mesatlantica</i>	*	*	*	Guinot
		<i>Alvinocaris</i>	aff. <i>markensis</i>		*		Saint-Laurent
		<i>Mirocaris</i>	<i>fortunata</i>	*	*	*	Segonzac
		<i>Chorocaris</i>	<i>chacei</i>		*	*	id
		<i>Rimicaris</i>	<i>exoculata</i>		*	*	id
		<i>Echinus</i>	<i>alexandri</i>		*		Sibuet
Echino- dermata	Echinida						
Chordata	Ophiurida	<i>OphiocTenella</i>	<i>acies</i>		*	*	Tyler
	Chondrichthyes	<i>Apristurus</i>	<i>maderensis</i>		*		Biscoito & Saldanha
		<i>Etmopterus</i>	<i>princeps</i>		*		id
		<i>CentrosCymnus</i>	<i>coelolepis</i>		*		id
		<i>Deania</i>	<i>profundorum</i>	*			id
		<i>Hydrolagus</i>	<i>affinis</i>		*		id
		<i>Hydrolagus</i>	<i>pallidus</i>		*		id
		<i>CataetYx</i>	<i>laticeps</i>		*		id
		<i>Chaunax</i>	sp.	*			id
		<i>Chiasmodon</i>	<i>niger</i>		*		id
		<i>Coelorhynchus</i>	<i>labiatus</i>		*		id
	Osteichthyes	<i>Epigonus</i>	<i>telescopus</i>	*			id
		<i>Gaidropsarus</i>	n. sp.	*	*		Biscoito, Saldanha & Desbruyères
		<i>Halosaurus</i>	<i>johnsonianus</i> ?			*	id
		<i>Guttigadus</i>	<i>latifrons</i> ?		*		id
		<i>Lepidion</i>	<i>schmidtii</i>	*	*	*	id
		<i>Lycenchelys</i>	n. sp.			*	Biscoito
		<i>Mora</i>	<i>moro</i>	*			Biscoito & Saldanha
		<i>Nezumia</i>	<i>sclerorhynchus</i>		*		id
		<i>Polyacanthonotus</i>	<i>rissoanus</i>		*	*	id
		<i>Simenchelys</i>	<i>parasitica</i>	*	*		id
		<i>Synaphobranchus</i>	<i>kaupi</i>	*	*		id
		<i>Trachyscorpia</i>	<i>cristulata echinata</i> *	*			id

were observed around these sites except a few small individuals of *Bathymodiolus azoricus* around the PP26 smoker. Two complex edifices (PP28/35 and PP37) were observed in the central part of the field. They were composed of several active (2–3) and inactive (5–10) chimneys. Temperatures measured at the diffuser summit ranged from 22 to 63°C. Low diffusion occurred along the lowest part of some clogging chimneys and all around the site through the sediment. These edifices were largely colonised by *M. fortunata* on sulphide diffusers with higher densities on chimneys covered by iron oxides (about twice as dense as on diffusers). Dense swarms of *R. exoculata* were located in small depressions between chimneys. At the PP37 site, a relatively large population of mussels had grown on the areas of low diffusion and on clogging chimneys. Small-sized mussels were located at the base of the chimneys where low diffusion occurred, while large-sized individuals were located on the higher parts of the inactive chimneys covered by deposits. About 20% of the mussels harboured the commensal polynoid *B. seepensis*. Along the active walls, a few bythograeid crabs (*S. mesatlantica*) were observed, as well as some zoarcid fishes among mussels at the base of the site. These proved to be a yet undescribed species of the genus *Lycenchelys*. Ophiurids, gastropods (*Phymorhynchus* n. sp.) and pygogonids also occurred in this sediment covered area. Small gastropods (*Mitrella nitidunila*, *Protolira valvatoides*, *Lepetrodrilus* n. sp., etc.), free polynoid and ampharetid polychaetes were sampled at this site (Table 3).

3.2. Site characterisation

In order to characterise the different microhabitats, we took a total of 70 discrete water samples and recorded temperatures in the main macrofaunal assemblages and within diffuse venting structures in the three vent fields. Within the LUCKY STRIKE vent field, three different sites (EIFFEL TOWER, BAIRRO ALTO and ELISABETH) were sampled. The averages and standard deviations of temperature, pH and concentrations of chemicals that fuel bacterial autotrophy are shown in Table 4. Cross comparisons between the fluids amongst habitats/sites were made using the Fisher test for variances and *t*-Student's test for means of small samples when $n \geq 4$ ($p = 0.05$). At the RAINBOW site, the microhabitats of *Rimicaris* and *Mirocaris* did not differ significantly. The microenvironment was significantly different for *Rimicaris* and *Mirocaris* vs. *Bathymodiolus* when methane content, pH and temperature were compared. The LUCKY STRIKE site was characterised by strong differences in the variances. The site-to-site comparison, concerning the mussels' microenvironment, revealed significant differences between RAINBOW, EIFFEL TOWER (LUCKY STRIKE), BAIRRO ALTO (LUCKY STRIKE) and MENEZ GWEN when pH was compared. Significant differences were also observed in the CO₂ and methane concentrations between EIFFEL TOWER and BAIRRO ALTO on one side and PP24 on the other. A decreasing gradient in ΣS , CO₂, CH₄ and temperature was found when these parameters were measured at the diffusers, in the *Rimicaris* and the *Mirocaris* habitats, in the mixed habitat of *Mirocaris* and *Bathymodiolus*, in the mussel beds and the seawater. However, when adjacent pairs of different habitats were compared, this gradient could not discern the microdistribution.

During the "VICTOR PREMIÈRE" cruise, the use of the in situ auto-analyser "ALCHIMIST" in the LUCKY STRIKE vent field allowed a better description of the vent population environment (Fig. 5 and Table 5). Profiles of temperature, sulphide and nitrate concentrations (Fig. 5) were obtained as the probe and inlet were gradually moved over the different animal populations within a quadrat (0.25 m²), terminating in an area of visible diffusion. The data obtained indicate general

Table 4

Mean values and standard deviations for chemical factors, temperature and pH as measured on discrete water samples at RAINBOW, LUCKY STRIKE and MENEZ GWEN vent fields. The data in bold type were not used in cross comparisons due to the small number of sample replicates

Site	Sample	<i>n</i>		T (°C)	pH	ΣS (μM)	CO ₂ (μM)	CH ₄ (μM)	NO ₃ ⁻ (μM)
RAINBOW PP 29	Diffuser	2	Mean	47.5	5.8	12.8	3791	112.4	15.4
			SD	3.5	0.4	13.4	251	31.4	0.4
	<i>Rimicaris</i>	9	Mean	13.2	6.8	8.5	2046	21.9	15.5
			SD	5.5	0.4	6.1	208	25.6	3.6
	<i>Mirocaris</i>	5	Mean	11.2	7.1	7.2	2219	6.5	17.1
			SD	4.0	0.3	8.7	383	4.3	0.7
LUCKY STRIKE Eiffel Tower	<i>Bathymodiolus</i>	5	Mean	6.0	7.7	3.8	2169	0.2	16.7
			SD	3.9	0.3	4.1	233	0.1	1.9
	Diffuser	5	Mean	29.3	6.4	18.8	408	61.9	16.3
			SD	29.9	1.0	30.6	2802	115.2	3.0
	<i>Bathymodiolus</i> + <i>Mirocaris</i>	11	Mean	6.8	7.3	2.4	2332	0.8	19.7
			SD	1.3	0.4	2.4	238	1.0	3.9
	<i>Bathymodiolus</i>	5	Mean	6.7	7.1	2.1	2430	0.0	18.3
			SD	3.0	0.2	1.4	152	0.0	0.5
	Seawater	1	Mean	4.4	7.79			0.0	20.03
			SD						
LUCKY STRIKE Bairro Alto	Diffuser	2	Mean	9.2	6.6	2.3	2209	0.3	17.1
			SD	4.0	0.6	3.1	401	0.3	0.8
	<i>Bathymodiolus</i> + <i>Mirocaris</i>	6	Mean	9.5	6.9	19.9	2737	0.2	17.9
			SD	3.4	0.4	14.7	238	0.2	0.5
	<i>Bathymodiolus</i>	6	Mean	6.7	7.2	1.2	2472	0.1	18.1
			SD	1.8	0.4	1.5	276	0.1	1.0
LUCKY STRIKE Elisabeth PP 24	Diffuser	2	Mean	85.0	5.3	155.7	2235	4.8	11.8
			SD	63.6	1.1	147.5	273	6.4	7.3
	<i>Bathymodiolus</i> + <i>Mirocaris</i>	1	Mean	13.7	6.31	2.78	2748	0.0	
			SD						
	<i>Bathymodiolus</i>	6	Mean	5.7	7.6	1.3	2086	0.0	
			SD	0.9	0.2	0.7	309	0.0	
MENEZ GWEN	<i>Bathymodiolus</i>	4	Mean	10.1	6.7	0.7			
			SD	0.5	0.2	0.4			

trends, as anticipated from discrete results (Table 5), but with a more precise definition of individual habitats. The mussels belonging to the youngest cohorts ("small mussels", shell length <30 mm) were present in environments where the temperature was ca. 5.4–7.6°C (Table 8) with small temporal variations. In this very diluted environment sulphide concentrations ranged from 0.7 to 1 μM. Cross comparisons (Fisher and *t*-Student's tests, $p = 0.05$) were performed using the in situ data obtained at the PP 24 vent site. The microhabitats described were significantly different from each other for the three parameters measured, with a continuous increase of temperature and ΣS and a decrease in nitrate from the small mussels' habitat towards the diffusers.

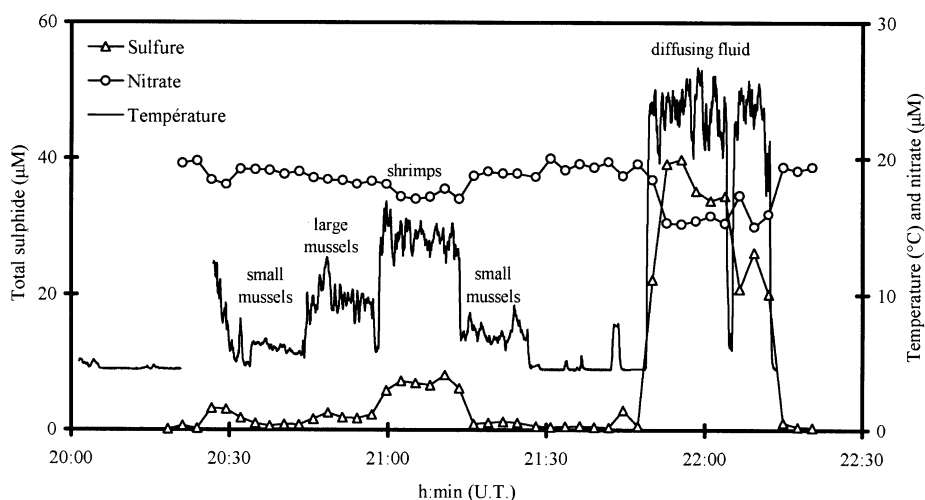


Fig. 5. Temperature (×), sulphide (Δ) and nitrate (○) concentrations experienced by different populations of organisms and recorded in situ by “ALCHIMIST”, in the LUCKY STRIKE vent field at Elisabeth PP24 site. “ALCHIMIST” is a chemical in situ analyser, based on flow-injection analysis and colorimetric detection.

Table 5

“ALCHIMIST” in situ temperature, sulphide and nitrate concentrations experienced by different species in the LUCKY STRIKE vent field at Elisabeth PP24 vent site

	<i>n</i>	T (°C)	Nitrate (μM)	Sulphide (μM)
Small <i>Bathymodiolus</i>	10			
Mean		6.5	19.0	1.0
SD		1.1	0.2	0.3
Large <i>Bathymodiolus</i>	4			
Mean		10.0	18.3	2.1
SD		1.2	0.1	0.4
<i>Mirocaris fortunata</i>	6			
Mean		13.9	17.4	6.9
SD		0.5	0.4	0.8
Diffuser	8			
Mean		22.6	15.6	31.2
SD		1.3	0.7	7.8

The metal concentrations amongst the different microhabitats displayed high variations due to the lack of distinction between particulate and dissolved metals. The mean values increase from seawater to mussel + shrimps environment (Table 6). The metal concentrations are at least one order of magnitude higher than those in seawater for Pb and Cu, two orders of magnitude higher for Cu.

Table 6

Metallic concentrations (total dissolvable metals) experienced by different communities as measured in discrete samples

		Sea water	Mussel beds	Mussel beds + shrimps
	N	3	20	10
Cu	Mean	7.1	104.3	237.6
$\mu\text{g l}^{-1}$	SD	0.8	112.5	350.9
Pb	Mean	0.9	10.1	17.5
$\mu\text{g l}^{-1}$	SD	0.4	10.8	27.7
Cd	Mean	0.3	1.0	3.4
$\mu\text{g l}^{-1}$	SD	0.1	1.3	5.8

Table 7

Processed temperature time-series (HOBO® and MICREL® temperature recorders). Ambient temperatures were 3.7°C in RAINBOW, 4.5°C in LUCKY STRIKE (L.S.) and 8.8°C in MENEZ GWEN

Site	Micro-habitats	Duration	Mean T (°C)	SD. T (°C)	Max T (°C)	Min T (°C)	ΔT_{max}
RAINBOW	<i>Bathymodiolus</i>	11 months	3.7	0.5	6.3	3.1	3.2
L.S./PP24	Small <i>Bathymodiolus</i>	11 months	5.5	0.7	9.6	4.2	5.4
L.S./PP24	Small <i>Bathymodiolus</i>	11 months	5.6	1.0	16.7	4.6	12.1
L.S./PP24	<i>Bathymodiolus</i>	11 months	12.8	3.7	25.5	4.8	20.7
L.S./Eiffel Tower	<i>Bathymodiolus</i>	1 month	6.4	0.8	10.5	4.5	6.0
L.S./Bairro Alto	<i>Bathymodiolus</i>	5 days	5.2	0.7	8.4	3.9	4.5
L.S./Bairro Alto	Small <i>Bathymodiolus</i>	5 days	6.6	0.9	9.1	4.0	5.1
L.S./Bairro Alto	<i>Bathymodiolus</i> and <i>Mirocaris</i>	5 days	8.2	1.7	14.2	4.6	9.6
L.S./Eiffel Tower	<i>Bathymodiolus</i> and <i>Mirocaris</i>	5 days	11.4	2.6	19.1	4.1	15
L.S./Eiffel Tower	<i>Bathymodiolus</i> and <i>Mirocaris</i>	5 days	14.4	3.0	24.6	6.0	18.6
L.S./Eiffel Tower	Diffuser	5 days	21.3	2.8	29.9	6.3	23.6
L.S./Bairro Alto	Diffuser	5 days	38.8	3.8	49.5	26.8	22.7
MENEZ GWEN	<i>Bathymodiolus</i>	1 day	9.6	0.4	11.7	8.3	3.4
MENEZ GWEN	<i>Bathymodiolus</i>	1 day	9.8	0.5	12.1	8.8	3.3

Temperature records covered a period ranging from a day to 11 months (Table 7). Temperatures varied considerably during the recording period. All the habitats, even those characterised by a mean temperature close to the ambient and by a reduced variability (e.g. mussel beds in RAINBOW or small mussel patches in LUCKY STRIKE), afforded significant temperature bursts (e.g. respectively 6.3 and 16.4°C). The comparison of the mean temperature values obtained during the first month with those obtained during the last month (11 months interval) showed a significant change. At PP24, a 5.9°C decrease in temperature was recorded among mussels. Inside large-sized mussel

Table 8

Elemental composition of particles collected in sediment traps at RAINBOW, LUCKY STRIKE, MENEZ GWEN and off-vent site (pelagic flux)

	Rainbow	Lucky Strike	Menez-Gwen	Pelagic flux
Mean total flux ($\text{g m}^{-2} \text{d}^{-1}$)	6.9	0.26	0.64	0.032
Organic carbon (%)	0.136	3.94	1.62	10.8
Inorganic carbon (%)	Not detected	3.48	0.98	8.0
Organic carbon flux ($\text{mg m}^{-2} \text{d}^{-1}$)	9.38	10.41	10.36	3.47
Nitrogen (%)	0.014	0.71	0.12	1.45
Sulphur (%)	17.24	10.76	18.17	0.54
Calcium (%)	26.6	10	26.2	—
Iron (%)	5.97	6.3	1.3	—
Copper (%)	3.59	0.93	0.5 detected	—
Barium (%)	0.25	3.19	1.7 detected	—

clumps at LUCKY STRIKE vent field, temperatures ranged from ambient to 25.5°C, i.e. the mean temperature of some diffusers.

Mean particle flux was $6.9 \text{ g m}^{-2} \text{d}^{-1}$ at RAINBOW and $0.26 \text{ g m}^{-2} \text{d}^{-1}$ at LUCKY STRIKE. At the MENEZ GWEN station, the trap on the mooring close to the vent sampled a steady flux of $0.64 \text{ g m}^{-2} \text{d}^{-1}$ over 10 days, and no difference was observed between the two sampling periods (5 days each). At the same time, the pelagic flux measured with the trap positioned off MENEZ GWEN hydrothermal field was $0.032 \text{ g m}^{-2} \text{d}^{-1}$. The main feature of the hydrothermal vent particles (Table 8) was the high concentration of sulphur (10.7–18.2%) in comparison with that of pelagic particles (0.5%). The organic carbon concentration was particularly low (0.14%) at RAINBOW. Barium concentration was high at MENEZ GWEN and Lucky Strike, whereas copper predominated at RAINBOW.

4. Discussion

Biogeography is influenced by local ecological and historical factors. Concerning the latter, hydrothermal-linked population homogeneity along an active ridge axis is conditioned by the presence or absence of “relay” sites between two fields and of major discontinuities (transform faults or continental plates). Distances between active zones are greater at slow spreading ridges than at fast ones, and thus exchanges between populations may be less frequent at the former. A linear model correlating the increase in the number of hydrothermal plumes with the increase of a ridge spreading rate has been proposed by Baker et al. (1995) and was recently re-examined following the discovery of many hydrothermal plumes along the South Western Indian Ridge, an ultra slow spreading ridge (Van Dover, 1998). German et al. (1996) have mapped seven hydrothermal plumes over 200 km of the Mid-Atlantic Ridge between 36 and 38°N. However, an unequivocal relationship between the presence of a plume and the existence of an active field could not be

established. In the present case (slow spreading ridge) distances between known fields in this area are relatively small (89 km between MENEZ GWEN and LUCKY STRIKE, 183 km between LUCKY STRIKE and RAINBOW) and therefore not in agreement with the above-mentioned model.

The first observations made at the shallower fields (850–1700 m) of the Azores Triple Junction, LUCKY STRIKE (Van Dover et al., 1993) and MENEZ GWEN (Desbruyères et al., 1994), contrast with those made on the southern and deeper fields, SNAKE PIT (23°N–3480 m) and TAG (26°N, 3650 m), as the former are dominated by mussels (*Bathymodiolus azoricus*) and the latter by shrimps, in particular *R. exoculata* (Rona et al., 1986; Galkin and Moskalev, 1990; Gebruk et al., 1993; Segonzac, 1992). This difference suggested the existence of isolation mechanisms, which could be either hydrostatic pressure thresholds or transform faults and fracture zones, and therefore the presence of two biogeographical provinces along the Mid-Atlantic Ridge, as proposed by Van Dover et al. (1993) and Desbruyères et al. (1994). Furthermore, the description of the fields of Broken Spur (29°N, 3000 m) (Murton et al., 1995; Copley et al., 1997) and Logatchev (14°45'N; 3000 m) (Gebruk et al., 1997) showed associations dominated by *R. exoculata* (Shank et al., 1998), thus confirming the dominance of shrimps in the fields south of the Atlantis Fracture Zone, deeper than 3000 m. Finally, the discovery of RAINBOW hydrothermal vent field at an intermediate latitude and depth (36°N, 2300 m) showed a situation more similar to that found at SNAKE PIT and BROKEN SPUR, with shrimps, especially *R. exoculata* and *M. fortunata*, present in great abundance at all active sites of the field. This intermediate situation, along depth and latitude gradients, is not in agreement with the two-provinces hypothesis referred to above.

The mussels present at RAINBOW vents belong to the same species as those at LUCKY STRIKE and MENEZ GWEN. Even though mussel populations are, at certain sites, rather abundant, they are located at the base of the edifices, as in the case of SNAKE PIT and rarely accommodate small individuals. Considering the dominant species and their relative contribution to the population composition, LUCKY STRIKE and MENEZ GWEN can be separated from other Mid-Atlantic Ridge fields. Moreover, taking all presently identified species and in spite of an apparent similarity between LUCKY STRIKE and MENEZ GWEN populations, the Jaccard index gives a low specific similarity (ca. 20% between MENEZ GWEN and LUCKY STRIKE). A similarity of the same magnitude is obtained between RAINBOW and MENEZ GWEN (20%) and is slightly higher between RAINBOW and LUCKY STRIKE (27%). Also, the specific similarity between RAINBOW and SNAKE PIT is low (22%) in spite of the general resemblance of both fields' communities. There is a remarkable difference in terms of similarity between fields, when the Atlantic is compared with the EPR. A similarity of over 40% is found between 13 and 21°N on the EPR. These two fields are ca. 1000 km away from each other and are separated by the Rivera and Orozco transform faults, but their depths (ca. 2600 m) are similar.

The main faunal differences observed between LUCKY STRIKE and MENEZ GWEN hydrothermal fields are due to a depletion of hydrothermal endemic species (respectively, 28 and eight endemic species) and to the penetration of bathyal species (40% in Rainbow, 72% in Menez Gwen), and therefore not to vicariance events. The populations of these two sites and those of RAINBOW are without doubt different because of a response to environmental conditions rather than geographic isolation mechanisms (Pico fault between LUCKY STRIKE and RAINBOW causes a 45-km long thrust).

In addition to the direct biological impact of hydrostatic pressure, bathymetric variations linked to the Azores hotspot presence produce a progressive change of the micro-hydrothermal

environment, not only among different fields, but also among sites within the same field, as in the case of LUCKY STRIKE vent field, under the action of phase separation phenomena. Additional chemical variations may also be associated with the presence of ultramafic rocks at RAINBOW. Nevertheless, in the same habitats in different vent fields, nutrient (H_2S and CH_4) and metallic ion concentrations and temperatures weakly vary, probably because of the organisms' specific requirements.

Within the vent fields, chemical analyses of discrete fluid samples were unable to significantly discriminate between the environments surrounding different shrimp species and mussels (except for the mussels at RAINBOW vent field). Two biases could jointly explain this inability: (1) mixing of microenvironments during sampling, (2) inadequacy of localisation of sample vs organism micro-habitat. Nevertheless, this set of data (plus the temperature time series) emphasises the variability of the microenvironment and the possible overlap between spatial distributions of individual species, and suggests the importance of inter-specific competition in the structuring of vent communities. In situ chemical analyses made at LUCKY STRIKE vent field (Eiffel Tower site) showed that a physical and chemical gradient does exist within the vent habitat. Caridean shrimps are the most eulithophilic organisms (Fustec et al., 1987), and adult mussel beds colonise the most diluted part of the gradient with the young individual clusters at the periphery (Sarradin et al., 1999). In RAINBOW vent field and Y3 (LUCKY STRIKE) segregation between the habitat of *R. exoculata* and that of mussels was also observed. *M. fortunata* and *C. chacei* were found to have a rather opportunistic distribution across the whole gradient. We can hypothesise that the presence of dense mussel beds covering the chimney walls at LUCKY STRIKE vent sites, which change the microenvironment (Johnson et al., 1994) and screen the sulphide wall, may preclude the development of *R. exoculata* swarms. This hypothesis must be tested in the future by experimental exclusion.

Even if *Bathymodiolus azoricus* harbours chemoautotrophic endosymbionts, it still has a filtering behaviour, not only for feeding from particulate organic matter (Le Pennec and Hily, 1984; Le Pennec and Prieur, 1984; Le Pennec et al., 1990), but also for providing its symbionts with methane or hydrogen sulphide and for respiration. The very high production of particles at Rainbow could negatively affect their filtering activity and then explain their relative exclusion from this field. When fed at high concentration of particles of low organic content, the shallow-water mytilids *Mytilus edulis* and *M. trossulus* can increase their filtration rate, reject a higher proportion of filtered material as pseudofaeces, and select organic-rich particles, thus maximising organic matter ingestion (Arifin and Bendell-Young, 1997; Bayne, 1976). However, the efficiency of such processes varies among bivalve species, and the feeding activity can be altered by high concentrations of inorganic particles, as in *Placopecten magellanicus* and *Mercenaria mercenaria* (Bricelj and Malouf, 1984; Cranford and Gordon, 1992). High particle concentrations could also affect juveniles, as Bricelj et al. (1984) demonstrated for *Mercenaria mercenaria*. Then we cannot reject the hypothesis that high concentrations of vent particles have a negative effect on *Bathymodiolus*, although the mechanisms are unknown. When particle concentration in the fluid decreases, filtering symbiotic species become dominant (LUCKY STRIKE and MENEZ GWEN vent fields).

Populations in the two shallower ATJ fields differ from those at other Mid-Atlantic Ridge sites, mainly because of the dominance of *Bathymodiolus azoricus*. RAINBOW field communities' composition and biodiversity, in spite of depth (2320 m) and the existence of transform faults (Haynes, Atlantis and Kane and Fifteen Twenty), are closer in structure to those of TAG, BROKEN SPUR and

SNAKE PIT. Chemical differences of the fluids surrounding organisms associated with the ultramafic rocks at the hydrothermal sites seem not to produce major faunal modifications. When particle concentration in the fluid decreases, filtering symbiotic species become dominant in relation to particle feeders and bathyal species penetrate in active areas to feed. The supposed time and space stability of sites at slow spreading ridges and the relative fragmentation of the environment give place to a weak specific similarity between sites, in terms of accompanying species. When comparing communities and environments at the three-studied vent fields on the ATJ, one cannot consider the existence of a single biogeographical province but rather a succession of several distinct biogeographic islands having different associations and habitats. Of course, one cannot rule out the existence of a direct effect of the pressure on the biological associations and metabolisms, although a large proportion of the bathyal species is known to be eurybathic between 800 and 2500 m. More likely, the hydrostatic variation leads to a rapidly varying habitat under phase separation processes within that bathymetric zone (ecotone patterns). At the shallowest vents, the hydrothermal fluid loses partly its toxic substances (dissolved and particulate metals and sulphide) but also a part of the nutrients fuelling the chemoautotrophic processes. We hypothesise that the decrease in fluid toxicity and physical aggressiveness allow “non-vent predators” to enter the hydrothermalism-affected area, to feed on remaining endemic species. This hypothesis may account for the decrease in number of non-endemic species with depth.

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