INTERACTIONS OF DEEP-SEA VENT INVERTEBRATES WITH THEIR ENVIRONMENT: THE CASE OF *RIMICARIS EXOCULATA*

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ABSTRACT The vent shrimp *Rimicaris exoculata* thrives around many hydrothermal vent sites along the Mid-Atlantic Ridge (MAR), where it aggregates into dense swarms. In contrast to hydrothermal vent fields at the East Pacific Rise (EPR), where the biomass is dominated by tubeworms, clams, and mussels, this shrimp is one of the major animal species at MAR vents. These animals are found in the dynamic mixing interface between cold oxygenated seawater and hot, reduced hydrothermal vent fluid. The adaptation of this shrimp to the hostile deep-sea hydrothermal environment and its survival strategy has been investigated since their discovery at the TAG site in the late 1980s. *Rimicaris exoculata* is now known to colonize black smoker complexes along the MAR in the depth-range of 2,300–3,900 m (Rainbow, Broken Spur, TAG, Snake Pit, Logatchev, 5°S (*Rimicaris cf exoculata*). Although the presence of the *Rimicaris* genus was first believed to be restricted to the MAR, a related species, *Rimicaris kairei*, was found recently at the Central Indian Ridge (CIR) (Edmonds and Kairei vent field). This review summarizes the current knowledge of *Rimicaris* shrimp, focusing on their spatial and temporal distribution, chemical and thermal environment, as well as on possible nutrition strategies and behavioral aspects. Recent studies suggested that iron oxide encrusted bacteria hosted in the branchial chamber of *R. exoculata* from the Rainbow vent field (MAR) might rely on iron oxidation. Striking results on the occurrence and morphology of iron precipitates, as well as on bacterial-mineral interaction in the gill chamber, have lead to the hypothesis of an iron-based symbiosis between bacteria and the shrimp. Special attention is called to these issues.

KEY WORDS: shrimp, Mid-Atlantic Ridge, hydrothermal vents, deep-sea, symbiosis, biomineralization, chemosynthesis, microorganisms, extreme environments

INTRODUCTION

Distribution of Rimicaris exoculata

The vent shrimp *Rimicaris exoculata* dominates the vagile fauna at most Mid-Atlantic Ridge hydrothermal vent sites (Fig. 1). This species lives within steep chemical and thermal gradients, where hot, reduced hydrothermal fluid mixes turbulently with oxygenated seawater. First described by Williams and Rona (1986), this species was observed to colonize black smoker complexes in the rift valley at the TAG site (26°08.3′N, 44°49.6′W; depth: 3,620–3,650 m). *Rimicaris exoculata* was subsequently found at several MAR-vent sites in the depth-range of 2,300–3,900 m (Rainbow, Broken Spur, TAG, Snake Pit, Logatchev, 5°S; Fig. 1, Table 1). In comparison with the hydrothermal environment on the East Pacific Rise where tubeworms, clams, and mussels dominate the vent fauna (Van Dover 1995), *Rimicaris exoculata* is by far one of the most abundant invertebrates at the Mid-Atlantic ridge vents (Williams & Rona 1986, Van Dover 1995, Van Dover et al. 2002, Desbruyères et al. 2000, Desbruyères et al. 2001). The two MAR-sites where this species has not been observed are the shallower vent fields Menez Gwen (860 m) and Lucky Strike (1,700 m). Although it was first believed that *R. exoculata* were present at the latter one (Van Dover et al. 1996), the existence of the shrimp at this site has not been reported after further expeditions (Table 1). Dense swarms of *Rimicaris cf. exoculata* were investigated at recently discovered hydrothermal vent fields along the southern Mid-Atlantic Ridge (Turtle Pits and Red Lion 5°S, 3,000m; References in Fig. 1 & Table 1). Recently, the existence of dense shrimp swarms at the active

Kairei and Edmond hydrothermal vent fields (Central Indian Ridge, 2,451–3,320-m depth) (Fig. 1, Table 1) was described (Hashimoto et al. 2001a, Hashimoto et al. 2001b). Van Dover et al. (2001) reported that shrimp tissue from these sites is isotopically indistinguishable from those of *R. exoculata* on the Mid-Atlantic Ridge. Further studies demonstrated that the shrimp found at the Central Indian Ridge are very close to *Rimicaris exoculata* but still clearly distinguishable by some morphological differences and therefore classified as *Rimicaris kairei* (Watabe & Hashimoto 2002).

The abundance of *R. exoculata* varies between different sites. For example, at Rainbow, shrimp assemble in depressions between chimney structures (Fig. 2B), whereas at TAG, black smoker complexes were almost entirely covered by dense agglomerations. Contrarily, at Broken Spur, low shrimp biomass was found (Copley et al. 1997). At the site Red Lion an unusual flange growth was investigated that appears to support a thriving shrimp community (Koschinsky et al. 2006). Other chimneys, that lack the flange growth, show a low abundance of *Rimicaris cf. exoculata* (Koschinsky et al. 2006). It is still unknown to what extent hydrothermal flow rates and composition influence the distribution of *R. exoculata*. However, they presumably play a role in the adaptation strategies of this species to such extreme environments. In particular, large variations in chemical composition of the endmember fluid have been observed between different MAR sites (Von Damm et al. 2001, Charlou et al. 2002, Douville et al. 2002).

Spatial Arrangement and Temporal Variation of Rimicaris exoculata *Swarms*

Rimicaris exoculata form large aggregations on solid sulfide surfaces around warm vent water emissions (Fig. 2). In
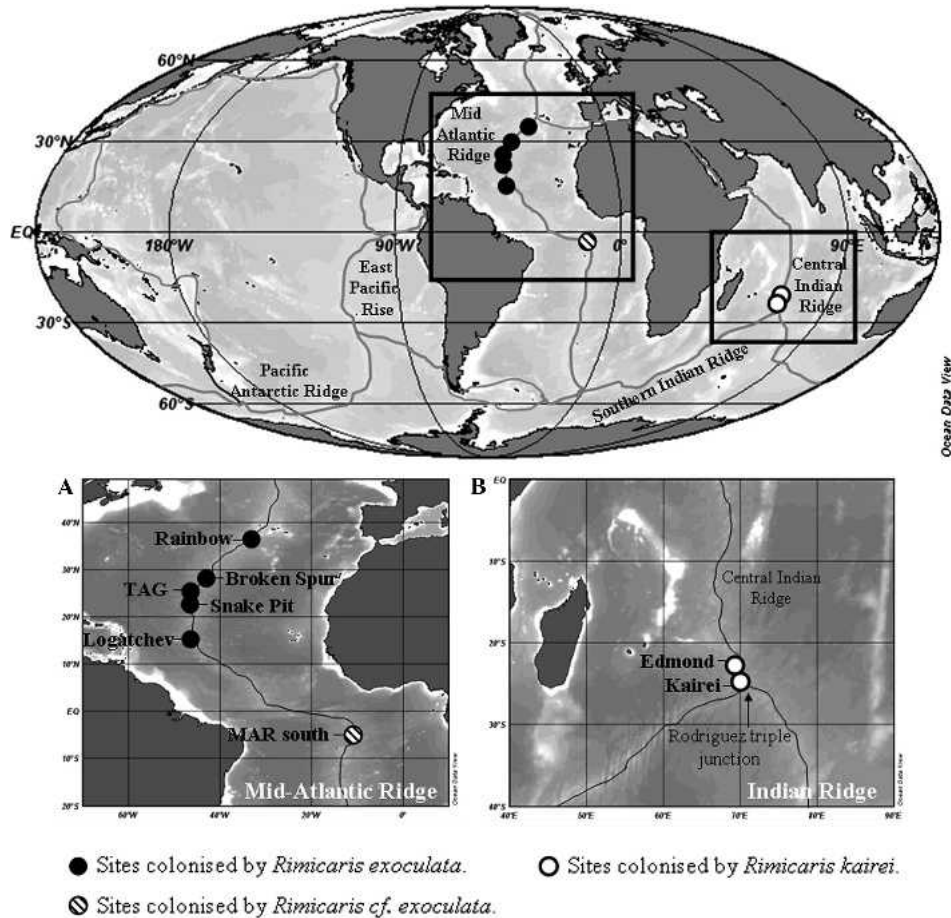
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Figure 1. **Global distribution of hydrothermal vent shrimp belonging to the genus *Rimicaris*. The occurrence of these shrimp at two ridge systems: (A) Mid-Atlantic Ridge (colonized by *Rimicaris exoculata* [black] & *Rimicaris cf. exoculata* [black-white]) and (B) Central Indian Ridge [colonized by *Rimicaris kairei* (white)] is indicated in the enlarged maps (for details, see Table 1).**

comparison with vents on the East Pacific Rise, little changes in faunal community composition have been observed for sites like TAG and Snake Pit, along the Mid-Atlantic Ridge (Van Dover 1995, Copley et al. 2007). For these sites, Van Dover et al. (1988) estimated an animal density of 2,000–2,500 ind·m^{-2}, whereas Gebruk et al. (2000a) stated abundances of 3,000 ind·m^{-2}. Recently, Copley et al. (2007) reported a mean animal density of 1,191 ind·m^{-2} (±326) for dives at TAG in 2004 using imaging techniques. Compared with dives at the same location in 1994, the abundance was in the same order of magnitude (1,120 ind·m^{-2} ± 474).

These high population densities were not found at Broken Spur (Copley et al. 1997). The absence of dense shrimp aggregations at this site, and the high ratio of predators and scavengers to primary consumers, were interpreted as an ecological instability, and possibly, recent environmental changes (Murton & Van Dover 1993). Murton et al. (1995) have suggested that venting at Broken Spur may have undergone a recent reactivation after a period of quiescence, and that animals were possibly recolonizing the environment (Van Dover 1995). Copley et al. (1997) proposed that the size of the *Rimicaris* populations and of the shrimp habitat may be a result of geological evolution of the venting structures. Shrimp abundance would be expected to increase to a similar extent as at TAG and Snake Pit. A significant level of gene flow has been detected

between *R. exoculata* populations at TAG and Broken Spur (Creasey et al. 1996). Hence, the presence of a metapopulation at these two sites was suggested, which in turn, could provide a colonization source after any interruption of venting. For other sites populated by *Rimicaris exoculata*, explicit studies on temporal variations of animal abundance have not yet been performed.

The substrate underlying the massive shrimp swarms was described as black sediments, orange-hued rocks with the appearance of polymetal sulfides originated from black smoker-type vents (Williams & Rona 1986) (Fig. 2). *Rimicaris exoculata* colonize smoker walls influenced by hydrothermal venting. Early studies described shrimp aggregations as a dense monolayer of adults on sulfide surfaces (Van Dover et al. 1988). Juveniles have been reported to occur in patches in slightly colder regions that are distinct from adult aggregations (Gebruk et al. 2000a). However, it was observed investigated in 2004 that juvenile shrimp assembled beneath closely-packed adults (Copley et al. 2007).

Rimicaris exoculata has been observed to swim back to the substrate when displaced from it (Van Dover et al. 1989, Gebruk et al. 1993). It was proposed that turbulent water currents might force the shrimp to actively maintain themselves in a sharply defined microenvironment, orienting against the hot fluid flow (Copley et al. 1997). The development of dense

TABLE 1.

Location of *Rimicaris exoculata* obtained from the literature.

site	Ridge system	Coordinates	depth (m)	species	Reference
TAG	MAR	26°N 44°W	3635–3670	*Rimicaris exoculata*	Williams & Rona 1986, Van Dover et al. 1988, 1989, Gal'chenko et al. 1989, Gebruk et al. 1993, Wirsen et al. 1993, Pond 1997a, Vereshchaka 1996, 1997, Shank et al. 1998, Rieley et al. 1999, Gebruk et al. 2000a, Vereshchaka et al. 2002, Copley et al. 1999, 2007
Snake Pit	MAR	23°N 44°W	3480	*Rimicaris exoculata*	Van Dover et al. 1988, 1989, Segonzac 1992, Casanova et al. 1993, Segonzac et al. 1993, Wirsen et al. 1993, Renninger et al. 1995, Polz & Cavanaugh 1995, Pond 1997a, Polz & Van Dover 1998, Gebruk et al. 2000a, Vereshchaka et al. 2002
Broken Spur	MAR	29°N 43°W	3050–3875	*Rimicaris exoculata*	Van Dover 1995, Murton et al. 1995, Copley et al. 1997, Vereshchaka 1996, 1997, Shank et al. 1998, Gebruk et al. 2000a, Pond 2000, Vereshchaka et al. 2002
Logatchev	MAR	14°N 44°W	2930–3020	*Rimicaris exoculata*	Gebruk et al. 1997, 2000a,b, Pond 2000, Fouquet pers. comm. 2007
Rainbow	MAR	36°N 33°W	2260–2350	*Rimicaris exoculata*	Gebruk et al. 2000a, Pond 2000, Compère et al. 0.2002, Vereshchaka et al. 2002, Ravaux et al. 2003, Zbinden & Cambon-Bonavita 2003, Zbinden et al. 2004, Gloter et al. 2004, Kadar et al. 2006, Schmidt et al. 2007, Gaill et al. 2007, Anderson et al. *In press*, Corbari et al. 2008, Zbinden et al. *submitted*
Kairei	CIR	25°S 70°E	2420–2460	*Rimicaris kairei*	Hashimoto et al. 2001a, Hashimoto et al. 2001b, Van Dover et al. 2001, Watabe & Hashimoto 2002, Gallant & Von Damm 2006
Edmond	CIR	23°S 69°E	3270–3320	*Rimicaris kairei*	Van Dover et al. 2001, Von Damm et al. 2001, Gallant & Von Damm 2006
MAR South (5°S)	MAR	5°S 12°W	2990–3050	*Rimicaris cf. exoculata*	Koschinsky et al. 2006, Haase et al. 2007

shrimp swarms could, therefore, rely on the availability of suf-ficient substratum surface, providing suitable microhabitat conditions. Recently, the study of Schmidt et al. (2008) sup-ported the idea that the fluid source feeding shrimp swarms is located below the animal assemblages rather than diffusing laterally from the wall of the hydrothermal smoker. This local source is described as a secondary vent fluid source on chimney flanks. It may already be mixed with seawater, and therefore, chemically different from the hydrothermal endmember fluid (Fig. 2A).

Although, the existence of *Rimicaris exoculata* was only proven for hydrothermal vent fields along the Mid-Atlantic ridge, this species must provide a good dispersal capability to overcome large distances between the individual sites (hundreds of kilometers). Because the shrimp are believed to feed in the upper water column during larval dispersal (Pond et al. 1997a, Pond et al. 2000), *R. exoculata* larvae may be passively trans-ported between deep-sea hydrothermal vent structures by water currents (Allen-Copley et al. 1998). Pond et al. (1997a) and Dixon et al. (1998) have shown that shrimp spend a substantial period of their early life stages as planktotrophic organisms in the water column before returning to suitable vent sites. They are feeding on photosynthetic material, to accumulate sub-stantial lipids for maturation.

Recently, Herring (2006) reported on shrimp postlarvae that were sampled at plume depth over the Kairei and Edmonds hydrothermal vent fields (South West Indian Ocean). They were morphologically indistinguishable from similar postlarvae sam-pled above vent sites along the MAR but supposed to belong to the adult *Rimicaris kairei*.

Temperature Range of Rimicaris exoculata *Habitat and its Thermal Tolerance*

The first studies at TAG approximately described the thermal range of *R. exoculata* to be between 10°C and 40°C (Van Dover et al. 1988, Gebruk et al. 1993, Segonzac et al. 1993) (Table 2). Later studies presented additional temperature data from the shrimp habitat at the Rainbow hydrothermal vent field (Desbruyères et al. 2000, Desbruyères et al. 2001, Geret et al. 2002) (Table 2). A precise investigation of the thermal habitat conditions of *Rimicaris exoculata* was realized for the Rainbow
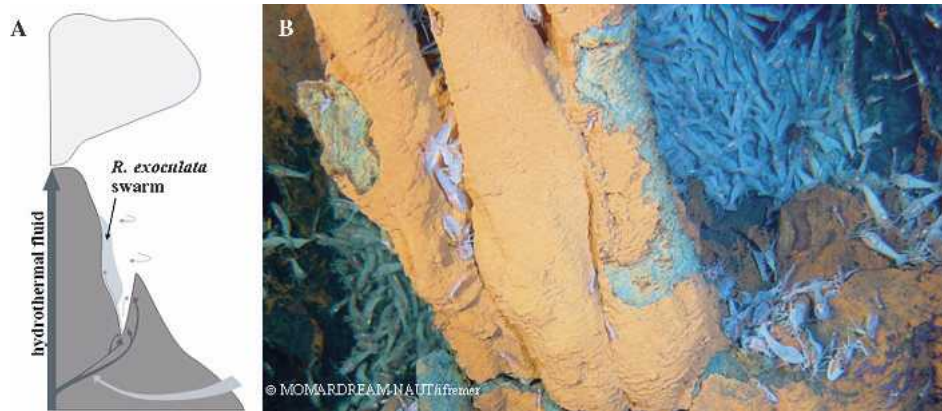
Figure 2. *In-situ* localization of the hydrothermal vent shrimp *Rimicaris exoculata*. **(A) Schematic representation of the shrimp environment and its general localization on a chimney complex as hypothesized in Schmidt et al. (2008). The swarm is positioned in the mixing zone between seawater and a local hydrothermal fluid source. (adapted from Schmidt et al. 2008) (B) Dense swarm of *R. exoculata* at the iron-rich hydrothermal vent field Rainbow (MAR) investigated during the MOMARDREAM-NAUT Cruise in 2007 (Gaill et al. 2007). Shrimp aggregate (typically at this site) in depressions hidden behind mineral spires.**

and TAG vent field by Schmidt et al. (2008) (Table 2). Temperature measurements were done all over the swarm and in the unpopulated surrounding. The T-probe was positioned as close as possible to the animals to register the accurate temperature of the shrimp habitat. Figure 3 represents schematically the thermal environment of shrimp swarms and their localization in the hydrothermal vent system (Schmidt et al. 2008). The temperature of the shrimp habitat at Rainbow and TAG ranged between 3°C and 18°C. The maximum temperature reported does not necessarily represent the upper limit of the shrimps' thermal habitat. However, it is consistent with molecular studies on the shrimps' stress response under heat exposure (Ravaux et al. 2003, Ravaux et al. 2007). This work showed that *R. exoculata* does not tolerate temperatures higher than 33°C and that a heat-inducible stress protein (hsp70) is already released at 25°C. Hence, the optimal thermal habitat may be restricted to temperatures below 25°C; significantly lower than suggested in earlier works (Gebruk et al. 1993, Van Dover et al. 1988, Segonzac et al. 1993) (Table 2). Juveniles that were observed to colonize colder zones away from high vent flow and black smoke emission (Gebruk et al. 2000a). In addition, Wirsen et al. (1993) demonstrated that the chemosynthetic activity of the shrimps' epibionts was distinctly higher at 20°C than at 50°C, suggesting optimum conditions for primary production at moderate temperatures. The boundaries of the narrow thermal range of the *R. exoculata* habitat may therefore be constrained by both the shrimp nutritional demands and their physiological thermal tolerance (Ravaux et al. 2003, Ravaux et al. 2007).

Chemical Environment of Rimicaris exoculata and its Exposure to Toxic Elements

Hydrothermal vent invertebrates are surrounded by fluids that are composed of numerous potential chemical threats, such as sulfide, methane and dissolved heavy metals (review in Childress & Fisher 1992, Van Dover et al. 2002, Le Bris & Gaill 2007). These vent organisms usually require specific adaptations to thrive in these metal/sulfide-rich, acidic and oxygen-depleted surroundings (Van Dover & Lutz, 2004). Hydrogen sulfide is a potential toxin for the aerobic respiration of living organisms (Visman 1991) Concentrations in the range of few micromolar, are normally toxic to many animals (Smith et al. 1979, Childress & Fisher 1992). Various hydrothermal vent species are continuously exposed to sulfide enriched fluids (review in Le Bris & Gaill 2007). Such conditions are required for the growth of sulfide-oxidizing microorganisms and are considered necessary to sustain mainly autotrophic carbon fixation for

TABLE 2.

Thermal characteristics of MAR vent sites hosting *Rimicaris exoculata*.

Site	Location	T (°C)	Reference
TAG	shrimp environment	20–30	Van Dover et al. 1988
	shrimp environment	10–40	Gebruk et al. 1993
	shrimp habitat	2.8–17.4	Schmidt et al. 2007
Snake Pit	shrimp environment	20–30	Van Dover et al. 1988
	shrimp environment	5–37	Segonzac et al. 1993
Logatchev	shrimp environment	>20	Gebruk et al. 1993
Rainbow	shrimp habitat	9–25	Desbruyères et al. 2000
	shrimp habitat	13.2	Desbruyères et al. 2001
	shrimp habitat	4.7–25	Geret et al. 2002
	shrimp habitat	3.2–18	Schmidt et al. 2008

study of hydrothermal tube worms, Cosson-Mannevy et al. (1988) hypothesized that a close relationship between bacterial activity and the accumulation of metals in the host tissue would constitute an alternative detoxification mechanism.

The chemical composition of the *Rimicaris* habitat varies strongly between the different sites (Table 3). Rainbow and Logatchev are located on peridotitic host rock, and their fluid are, therefore, distinctly enriched in dissolved gases, like methane and hydrogen (Fig. 4). In contrast, hydrogen sulfide concentrations are low at these sites, in comparison with basalt hosted vent systems Broken Spur, TAG, and Snake Pit. Figure 4 displays the endmember chemistry of vent sites that are colonized by *Rimicaris* (references to the corresponding studies are listed in Table 3 and the figures are designed as already presented in Desbruyères et al. 2000 including more recent data of sites at the Central Indian Ridge). Another chemical feature of the Rainbow site is the extreme enrichment in dissolved metals (e.g., Fe, Cu, Zn, Mn). The concentrations found here are the highest observed in the MAR hydrothermal area (Charlou et al. 2002, Douville et al. 2002). The chemical composition of the endmember fluid at Kairei and Edmond vent field lies in the same range as those for the MAR sites. Both sites are low in methane, similar to the MAR vent fields TAG, Snake Pit, and Broken Spur (Fig. 4). However, the hydrothermal fluid at the Edmond field constitutes an elevated iron concentration (13.9–10.7 mM), which is roughly half the concentration found at Rainbow but distinctly higher than at all other MAR sites. The sulfide amounts at this site range between those measured at Rainbow and Snake Pit or TAG (Fig. 4 & Table 3).

It has been argued that the natural long-term exposure of hydrothermal shrimp to elevated concentrations of toxic elements may have provoked the evolution of efficient metal handling strategies (Geret et al. 2002, Martins et al. 2000).

Figure 3. Schematic representation of a hydrothermal vent hosting shrimp swarms, their location in the system and the local thermal condition (data represent measurements taken at different hydrothermal vent sites, see Table 2 & 3), (adapted from Schmidt et al. 2008).

invertebrate communities, both, in free-living forms or in symbiotic relationships with host animals. Other potential poisons to which hydrothermal vent organisms are exposed at high levels are dissolved transition metals, such as copper, zinc, cadmium, or lead. High tolerance to soluble, toxic metal compounds is expected among mesophilic organisms that colonize ecological niches in vent systems (Vetriani et al. 2005). In a

TABLE 3.

Chemical data of the MAR sites hosting *Rimicaris exoculata*.

	T (°C)	pH	H$_2$S (mM)	CH$_4$ (mM)	H$_2$ (mM)	Fe (mM)	Cu (μM)	Zn (μM)
Endmember								
TAG	270–369	3.4–2.5	6.7–2.5	0.62–0.12	0.37–0.15	5.56–1.64	150–83	46
Snake Pit	335–356	3.9–3.7	6.1–2.7	0.062–0.023	0.48–0.19	2.56–1.8	35–10	53–47
Broken Spur	356–364	—	11.0–8.5	0.13–0.065	1.03–0.43	2.16–1.64	69.6–28.3	88.0–40.8
Logatchev	347–352	3.9–3.3	2.5–0.5	3.5–2.1	19.0–12.0	2.5–2.4	50–15	36–25
Rainbow	360–365	3.1–2.8	2.5–1	2.5	16	24	162–121	185–115
MAR south	400–408	—	—	0.03–0.02	0.29–0.08	—	—	—
Kairei	315–365	3.51–3.35	4.16–4.02	0.207–0.175	8.38–8.07	6.15–3.62	282–120	91.5–68.0
Edmond	273–382	3.02–2.97	4.92–1.02	0.424–0.295	0.254–0.002	13.9–10.7	412–113	152–125
Shrimp swarm								
TAG	2.8–17.4	8.1–6.8	0.0005–0.027	0.0001–0.0057	—	0.0028–0.14	—	—
Rainbow	4.7–25.0	7.8–6.3	0.0004–0.022	0.021*	—	0.058–1.470	0.14–3.20	—
Seawater	2	7.8	~0	<0.0003	<0.0004	<0.0045	<0.007	<0.028

* mean values for T = 13.2°C.
Endmember–Rainbow: Charlou et al. 1997, 2002; Donval et al. 1997; Douville et al. 2002; **TAG**: Charlou & Donval 1993; Von Damm 1995; Edmonds et al. 1996; Rudnicki & Elderfield 1992; Charlou et al. 1996; Gamo et al. 1996; Douville et al. 2002; Chiba et al. 2001; **Broken Spur**: James et al. 1995; Lein et al. 2000; **Snake Pit**: Von Damm 1995; Campbell et al. 1988; Jean-Baptiste et al. 1991; Edmond et al. 1995; Rudnicki & Elderfield 1992; Douville et al. 2002; **Logatchev**: Charlou et al. 1998; Douville et al. 2002; Schmidt et al. 2007; **MAR-South**: Koschinsky et al. 2006; Haase et al. 2007; **Kairei**: Gamo et al. 2001; Von Dover et al. 2001; Gallant & Von Damm 2006; **Edmond**: Van Dover et al. 2001; Von Damm et al. 2001; Gallant & Von Damm 2006; **Seawater**: Douville et al. 2002; Charlou et al. 2002; Gallant & Von Damm 2006; **Shrimp environment**: Desbruyères et al. 2001; Geret et al. 2002; Schmidt et al. 2008.
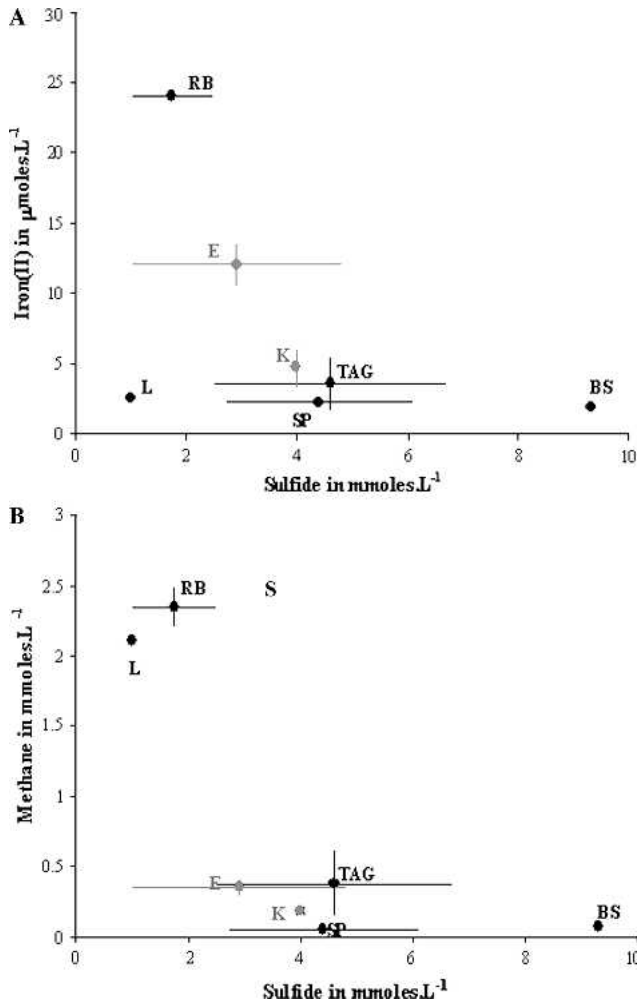
Figure 4. Chemical variation of the endmember fluid at different hydrothermal vent fields at the Mid-Atlantic Ridge (black) and the Central Indian Ridge (grey) colonized by *Rimicaris exoculata* and *Rimicaris kairei*, respectively: (A) Iron (II) as a function of sulfide concentration; (B) Methane as a function of sulfide concentration. Sulfide values represent the total concentration of dissolved S^{-II}. (K: Kairei, E: Edmond vent field, RB: Rainbow, L: Logatchev, SP: Snake Pit, BS: Broken Spur; MAR south insufficient data set) (References to the corresponding studies are listed in Table 3 and the figures are designed as already presented in Desbruyères et al. (2000) including more recent data of sites at the Central Indian Ridge.)

These specific mechanisms prevent acute toxicity and enable the shrimp to survive in extreme vent environments. Based on electron microscopy analysis, Compère et al. (2002) hypothesized that transport and detoxification processes may occur in the shrimps' gill chamber, where bacteria could detoxify the fluid using sulfide in their chemosynthetic activity. Toxic heavy metals and radioactive elements originating from the hydrothermal fluid, may adsorb on iron oxide deposition (Cornell & Schwertmann 2003). This removal of chemical compounds lowers the quantity of toxics that will be taken up by vent animals.

Morphological and Behavioral Features of Rimicaris exoculata

Rimicaris exoculata is a Caridean shrimp (Williams & Rona, 1986). First studies presented *R. exoculata* as a completely eyeless species (Williams & Rona, 1986). This raised the question how the shrimp coordinate their movement. Van Dover et al. (1989) showed that the vent shrimp *Rimicaris exoculata* has a thoracic eye that is well adapted for the detection of dim light. Thermal radiation from high-temperature plumes at black smoker chimneys could provide the electromagnetic signal sensed by the shrimp. Herring et al. (1999) suggested irretrievable damage of the sensitive thoracic eye on shrimp sampled at the Mid-Atlantic ridge caused by high-intensity floodlights of submersibles. Based on previous studies Renninger et al. (1995) proposed that chemicals in the hydrothermal fluid may serve as attractants, suggesting that the shrimps' active movement is driven and directed by a chemosensory response.

An additional morphological feature of *R. exoculata* is its hypertrophied branchial cavity (Fig. 5) (Segonzac et al. 1993) and the associated microflora colonizing this cavity (Fig. 6). Microbial filaments were observed to cover legs, gills, and parts of the carapace, particularly the underside of the cephalothorax (Van Dover et al. 1988, Segonzac et al. 1993). The surfaces appear rusty brown, or even black due to precipitated minerals and metal-compounds (Wirsen et al. 1993, Gebruk et al. 1993). Zbinden et al. (2004) emphasized that bacteria in the branchial cavity of shrimp sampled at Rainbow were primarily associated with rusty precipitates (Fig. 5). These authors found a heterogeneous spatial distribution of bacteria and minerals. Three distinct compartments were defined: (1) a lower prebranchial chamber with bacteria but devoid of minerals; (2) a gill chamber without bacteria and without minerals; and (3) an upper branchial chamber with a ectosymbiotic bacterial community associated with mineral deposits (Fig. 5).

Juvenile shrimp can be distinguished from adults by their bright orange color (Shank et al. 1998). They contain substantial pigmented lipid reserves, which are distinctly visible under their carapace. Shank et al. (1998) demonstrated that these "orange" shrimp, first believed to constitute a separate species (Vereshchaka 1996), are juvenile *Rimicaris exoculata*. Pond et al. (2000) analyzed gray-white adult shrimp to find back the juvenile lipid storage. In their studies, neither small nor large adult shrimp contained these substantial lipid reserves.

Nutrition Strategy of Rimicaris exoculata

One of the main research interests since the discovery of *Rimicaris exoculata* and its vast distribution along the Mid-Atlantic Ridge is investigations into its feeding behavior and survival strategy. Three main dietary carbon sources were suggested: (1) epibionts, (2) bacteria associated with sulfide particles originating from the black smoker complexes, and (3) detritus from the oceanic photic zone. The shrimps' life cycle contains different morphological stages with different nutritional strategies. The life cycle begins as a pelagic larvae, changes to a scavenger juvenile stage, and then finally becomes the symbiont-bearing adult stage (Kadar et al. 2006).

By means of gut content analyses, Van Dover and colleagues (1988) suggested that the shrimp grazes on free-living microorganisms affiliated with black smoker chimneys. Large amounts of sulfide particles from the vent solid surfaces were found in the animal's gut. It was inferred that high bacterial productivity would be required to sustain the massive populations of *R. exoculata*. These authors hypothesized a second nutritional source
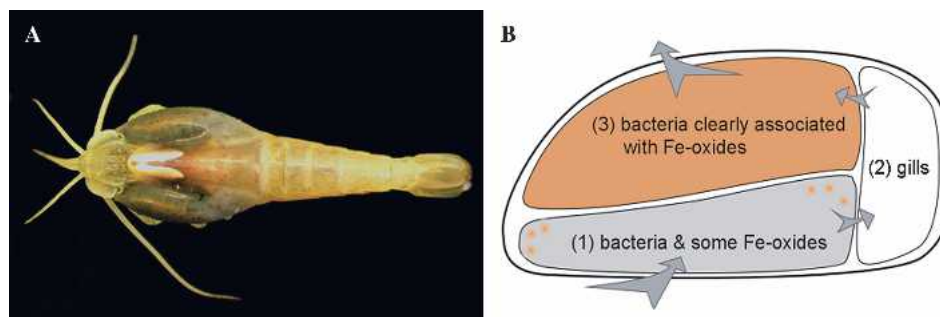
Figure 5. *Rimicaris exoculata* **(A) sampled during the MOMARDREAM-Naut Cruise in 2007 at the Rainbow vent field (scale 1cm), and a schematic representation of its branchial cavity (B) showing three distinct compartments (after Zbinden et al. 2004). Bacterial colonization and a lack of major iron oxide formations characterize the prebranchial chamber (1). In the gill chamber (2) neither bacteria, nor minerals were found. In the third compartment (3) dense bacterial populations were investigated found to be closely associated with iron oxides. The arrows indicate the stream direction of moving fluid through the branchial chamber.**

provided by the epibiotic microorganisms that densely coat its chelae. No evidence for chemoautotrophic endosymbionts associated with *R. exoculata* was shown with these preliminary studies.

One of the prime conclusions of the work done by Segonzac et al. (1993) was that shrimp seemed to fill most of its nutritional needs from the epibiotic bacteria in the prebranchial chamber. Gebruk et al. (1993) supported this hypothesis and showed that the standing crop of free-living bacteria in the water column above shrimp swarms or on mineral surfaces at TAG was not enough to sustain such high populations. Moreover, high
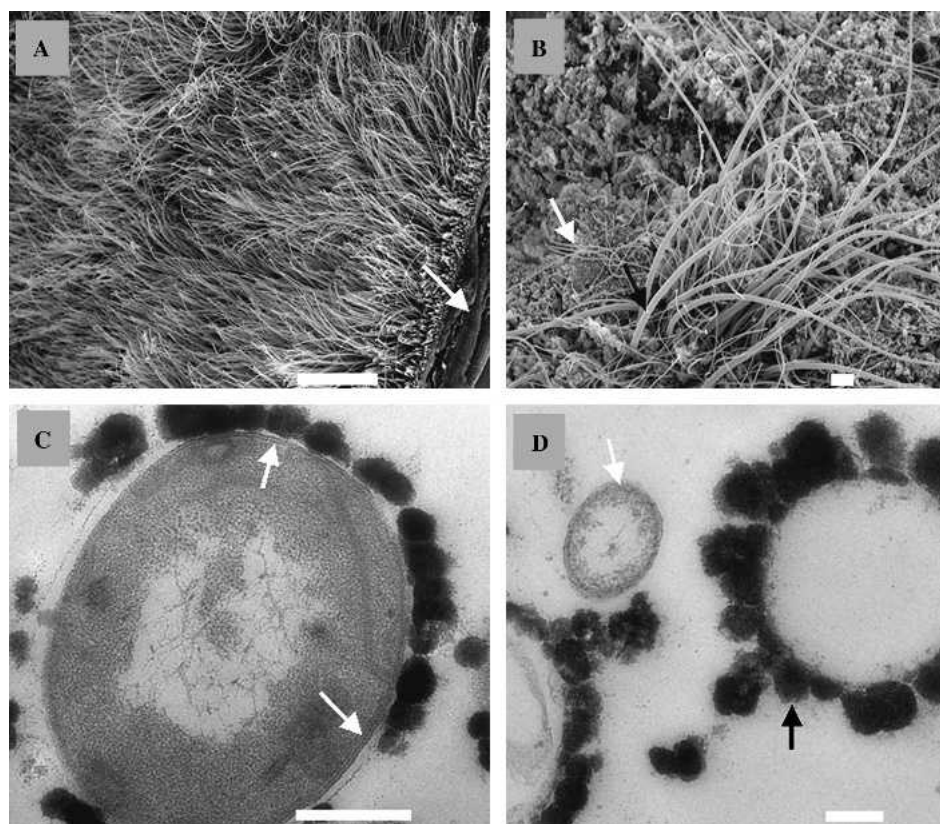

Figure 6. Morphology of bacteria associated with the shrimp integument in the third compartment (see Fig. 2) of its branchial cavity. (A) General view of filamentous bacteria attached to the shrimps cuticle (see arrow) and associated with mineral precipitates (scale: 100 μm) (SEM). (B) Higher magnification of the microorganisms embedded in dense iron oxide clusters (scale: 10 μm). Two types of filamentous bacteria are present that differ in size (black arrow: thick bacteria; white arrow: thin bacteria). (SEM) (C) Transverse section of a filamentous bacteria associated with iron oxide clusters (scale: 200 nm). Bacterial cellular structures are well preserved (i.e., double membrane, see flash). (TEM) (D) Transverse section of two bacteria differing in diameter (scale: 500 nm). The thinner bacteria (white flash) totally lacks iron oxides clustering on its cell membrane. For the thicker one (black arrow) no cellular structures are visible in the bacteria, that is surrounded by dense agglomerations of iron oxides, suggesting that this microorganism is dead. (TEM). (Images are taken by L. Corbari (A & B) and L. Anderson (C &D) using the techniques described in the corresponding publication (Corbari et al. 2008, Anderson et al. in press)

enzymatic CO_2 reduction in bacterial filaments that cover the inner surface of the shrimp carapaces were investigated by Jannasch et al. (1991), suggesting a key role of exosymbiotic bacteria in chemosynthetic carbon fixation based on sulfide oxidation (Gebruk et al. 1993, Wirsen et al. 1993). Casanova et al. (1993) proposed that shrimp might adsorb dissolved organic matter from these bacteria. Consistent with these hypotheses, Rieley et al. (1999) demonstrated by means of stable isotope composition and fatty acid analysis that shrimp from Snake Pit and TAG hydrothermal vent fields derive most of their organic carbon from epibiotic bacteria associated with their carapaces. Polz et al. (1998) proposed an alternative nutritional pathway and suggested that active autotrophic bacteria in the gut, that are isotopically similar but phylogenetically different from each other, may contribute to the overall nutrition of *R. exoculata*. These results were confirmed by Zbinden and Cambon-Bonavita, (2003)Additionally, the discovery of crustacean cuticular fragments in the gut of *R. exoculata* (Segonzac et al. 1993) and the analysis of digestive enzymes (Ravellec & Van Wormhoudt 1997) suggested a low potential for necrophagy.

Several studies suggested that the shrimp community is sustained by different nutritional sources, such as chemosynthetic and photosynthetic derived ones. By means of stable carbon isotopes, Van Dover et al. (1988) demonstrated that adult shrimp indeed depend on nonphotosynthetic organic carbon sources, whereas their nitrogen isotopes are consistent with a role as primary consumers. However, planktonic larval feeding is necessary for the accumulation of essential fatty acids required for maturation and breeding (Pond et al. 1997a, Pond et al. 1997b, Pond et al. 1997c, Pond et al. 2000). Particulate dissolved organic matter of photosynthetic origin may represent an appropriate nutritional source. In that case, *Rimicaris exoculata* is similar to the majority of marine animals that depend to a certain degree on organic compounds produced in the surface layers of the ocean and otherwise on the chemosynthetic food sources available in deep-sea hydrothermal environments (Pond et al. 2000).

Mineral Deposits in the Branchial Chamber of Rimicaris exoculata

The presence of mineral sulfide particles (agglomeration of dark minerals) associated with bacteria on the body parts of *R. exoculata* was described for the TAG hydrothermal vent field (Gebruk et al. 1993, Wirsen et al. 1993). Later studies reported on the occurrence of rusty precipitates in the branchial chamber of shrimp sampled at Rainbow (Zbinden et al. 2004). Microscopic analysis revealed a heterogeneous spatial distribution of bacteria and minerals (see section 5) (Fig. 5). Corbari et al. (2008) reported that bacterial colonization strongly depends on the molt stage of the animal, because bacteria are directly anchored to the cuticle (Fig. 6). Bacterial recolonization and reprecipitation of minerals on new cuticle surface occurs after each molt. The grain size within the mineral crust gradually increases away from the bacterial surface and the cuticle. Corbari et al. (2008) therefore suggested that the iron oxide formation is continuously initiated from below. The mineral clusters associated with the shrimps' bacterial community were microscopically analyzed and defined to be mostly composed of two-line ferrihydrite (Gloter et al. 2004, Anderson et al. in press). By means of extensive microscopic studies, it was shown

that initial iron oxides are formed after bacterial colonization in close contact with cell walls or their mucous sheath (Zbinden et al. 2004, Anderson et al. in press, Corbari et al. 2008) (Fig. 6), that would prevent bacteria from encrustation and support the continuous metabolic exchange through the cell membrane (e.g., Crundwell 2003, Chan et al. 2004, Fortin & Langley 2005).

Currently, the specific role of the associated bacterial community in the host survival strategy remains unknown. Several studies have hypothesized that bacteria may contribute to the animals' nutrition and detoxification mechanisms in these extreme environments. Variations in the specific composition and abundance of these iron minerals may be directly related to different chemical environments along the MAR. However, considering the lack of iron oxides in the lower prebranchial chamber of shrimp sampled at Rainbow, the described detoxification process will not be effective for the respiratory organs (Zbinden et al. 2004).

Diversity and Putative Activity of Epibionts

Cultivation of the epibionts has not yet been successful, hampering the exact determination of the microbial metabolic activity. After the first phylogenetic analysis of Snake Pit samples, Polz and Cavanaugh (1995) concluded that the epibiont community consists of only one single bacterial phylotype belonging to ε-Proteobacteria. They were assumed to be sulfur-oxidizing bacteria. Recent microscopy studies (Zbinden et al. 2004) have yielded the hypotheses that iron oxidation may represent a significant carbon fixation pathway in the shrimp environment at Rainbow. The morphology of abundant iron oxides (Gloter et al. 2004; Anderson et al. in press, Zbinden et al. submitted), their formation mechanism and association with bacteria (Corbari et al. 2008) (Fig. 6), and their distribution in the branchial chamber of *Rimicaris exoculata* (Zbinden et al. 2004) (Fig. 5) led to the idea of an iron-based symbioses. These authors suggested that modification of physicochemical conditions downstream, the gills could influence bacterial metabolisms. Particularly, a potential decrease in oxygen would favor the development of bacterial iron oxidizers in the postgill compartment. This would constitute an unique metabolism in deep-sea hydrothermal environments, where symbiotic relationships rely mostly on methane and sulfide as energy sources.

A theoretical approach comparing main chemical energy sources for chemosynthetic microorganisms in the environment of *R. exoculata* at Rainbow and TAG was proposed by Schmidt et al. (2008). This study demonstrated that at Rainbow iron oxidation provides the highest energy budget in the interfacial zone where the shrimps are located. Methane oxidation appears as a second potential energy source, whereas sulfide oxidation remains insignificant in the overall energy budget. Under the assumption that hydrogen will not be fully depleted by its abiotic oxidation in the shrimp environment, it may provide an additional significant energy source for bacteria (Schmidt et al. 2008). These results further support the hypothesis of an existing iron-based symbiosis associated with *Rimicaris exoculata*.

In contrast to the Rainbow vent field, sulfide oxidation was determined to provide the maximum energy available for chemoautotrophic mechanisms at TAG, consistently with the assumption made from previous biological studies (i.e., Van Dover et al. 1988, Gebruk et al. 1993, Wirsen et al. 1993). Here,

methane oxidation was shown to be of minor importance in terms of bioavailable energy. The early work of Gal'chenko et al. (1989) reported that no evidence for methane oxidation or assimilation of methane carbon in any of the shrimp tissue samples from TAG site.

In summary, these findings support the idea that diverse chemosynthetic pathways could fuel highly productive *Rimicaris exoculata* communities in the MAR vent environment. The transfer of geothermal energy between rich populations of host animals and a bacterial community may follow different routes at different distant deep-sea locations (Jannasch & Mottle 1985, Wirsen et al. 1993).

Perspectives on Future Work

The oxidation of iron may constitute an underestimated source for autotrophic carbon fixation in deep-sea hydrothermal environments (Emerson & Moyer 2002, Bach & Edwards 2003, Edwards et al. 2003). Until now, a symbiotic relationship between iron-oxidizing bacteria and large invertebrates has not yet been demonstrated. Cultivation of the microbial community associated with *Rimicaris exoculata* could provide insights on the question of whether the shrimps' nutritional needs are (partly) met by iron oxidizing symbionts or not. Another important issue is the relative contribution of different metabolisms. Other epibionts (methane-, sulfide-, hydrogen-oxidizers) may contribute to or may dominate (i.e., at vent sites other than Rainbow) the energy acquisition (Zbinden et al. submitted). Kinetic studies on the chemical reactions and their constraints on the availability of electron donors (particularly hydrogen) would provide further information on the competition between abiotically and biologically-driven processes in this dynamic environment. Getting insights into these matters, could improve the knowledge on the adaptability of *Rimicaris exoculata* to different deep-sea hydrothermal environments. Future studies should also focus on dispersion and colonization behavior of the shrimp. Why *Rimicaris exoculata* is only found along the Mid-Atlantic Ridge (with the exception of the similar species *Rimicaris kairei* at the Central Indian Ridge) is still an open question. Additionally, *Rimicaris exoculata* abundance varied between the vent sites from dense swarms covering the whole chimney structure (TAG) to random patches of shrimp aggregations (Broken Spur). Colonization processes and ecological impacts of environmental changes remain the scope of future research.

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