ORIGINAL ARTICLE

Adaptation to metal toxicity: a comparison of hydrothermal vent and coastal shrimps

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Abstract

Rainbow vent field is one of the most metal-contaminated hydrothermal sites on the Mid-Atlantic Ridge near the Azores region. Two hydrothermal shrimp species dominate the fauna at the Rainbow site along with the mussel *Bathymodiolus azoricus*. Although the levels of essential and non-essential metals in these shrimps have been studied, the biological consequences of a metal-rich environment are still largely unknown. Therefore, the aim of this study was to determine the levels of metal-binding proteins – metallothioneins (MT) and the activities of antioxidant enzymes – superoxide dismutase, catalase, total glutathione peroxidase and selenium-dependent glutathione peroxidase in two hydrothermal vent shrimps (*Mirocaris fortunata* and *Rimicaris exoculata*) collected from the Rainbow site and to compare them with two coastal shrimps (*Palaemon elegans* and *Palaemonetes varians*) from a south Portugal lagoon (Ria Formosa) to evaluate their different adaptation strategies towards metals in their environment. Results show significant differences in MT levels and antioxidant enzymatic activities between vent and coastal shrimps and also between shrimp species collected from the same site. This suggests that biochemical responses in both vent and coastal shrimps are affected not only by the environmental characteristics but also by inter-specific differences. Nevertheless, these responses apparently confer successful adaptation for survival in a metal-extreme environment.

Problem

Hydrothermal vent environments exhibit natural high metal concentrations as a result of the interaction between seawater and magmatic rocks. Consequently, the hydrothermal vent fluids have a very high temperature (300–350 °C) and are naturally enriched in silica (SiO_2), metals (*e.g.* Fe, Mn, As, Cd, Cu, *etc.*) and dissolved gases (*e.g.* H_2S, CH_4, H_2, CO_2) (Von Damm 1990, 1992; Lowell *et al.* 1995; Von Damm *et al.* 1995; Sarradin *et al.* 1998).

The Rainbow vent field was discovered in 1997, is located at 36° 13.8′ N 33° 54.15′ W in the north AMAR (ALVIN Mid-Atlantic Ridge) segment, and is the deepest vent site located in the Azores Triple Junction area (2270–2500, 2320 m deep) (Fouquet *et al.* 1997; Desbruyères

et al. 2001; Douville *et al.* 2002). The most active smokers are located at the western and the eastern ends of the hydrothermal field (Desbruyères *et al.* 2001). Rainbow hydrothermal fluids are uniform in composition and influenced by phase separation (Douville *et al.* 1999). Active chimneys, emitting hot-temperature (365 °C) acidic fluids (pH = 2.8) and that are relatively low in H_2S, are arranged longitudinally along a 200-m stretch of ridge. The metal concentrations (Cu, Fe, Mn, and Zn) in Rainbow vent fluids are the highest observed in the MAR hydrothermal area (Desbruyères *et al.* 2000; Douville *et al.* 2002).

In contrast, the Ria Formosa is a highly productive mesotidal lagoon, separated from the ocean by a system of five sand barrier islands and six inlets, which extend for about 55 km along the south coast of Portugal.

The average water depth is <2 m and the tidal height varies from a maximum of 3.7 m at spring tide to a minimum of 0.4 m at neap tide. Hence, most of the water volume is drained in each tidal cycle, thereby imposing a short residence time and an intense exchange of materials between the Ria Formosa and the adjacent coastal waters (Bebianno 1995; Caetano *et al.* 2002; Santos *et al.* 2004). Nevertheless, the water quality of the lagoon has deteriorated over the last decade reflecting the intense economic development of areas around the lagoon, whose major inputs of pollutants came from untreated sewage and domestic effluents from two cities (Bebianno 1995; Caetano *et al.* 2002).

Caridean shrimps, in particular *Mirocaris fortunata* (Martin & Christiansen 1995) and *Rimicaris exoculata* (William & Rona 1986), co-dominate populations in deep Atlantic hydrothermal fields near the Azores Triple Junction. The shrimp species *M. fortunata* colonize mainly sulphide diffusers, with higher densities on chimneys covered by iron oxides. In contrast, dense swarms of *R. exoculata* are located in small depressions between chimneys expelling superheated sulphide-loaded fluid (Gebruk *et al.* 1993, 2000; Segonzac *et al.* 1993; Polz *et al.* 1998; Desbruyères *et al.* 2001). These species have been extensively studied in terms of their abundance, density and microhabitat preferences in MAR hydrothermal vents (Gebruk *et al.* 1993, 2000; Segonzac *et al.* 1993; Desbruyères & Segonzac 1997; Polz *et al.* 1998), behaviour and nutritional strategies (Casanova *et al.* 1993; Renninger *et al.* 1995; Gebruk *et al.* 2000) and concentration of essential and non-essential metals in their tissues (Geret *et al.* 2002; Kádár *et al.* 2006). Nevertheless, the physiological responses towards metals in these species are still largely unknown. It is well recognized that metals can be toxic to organisms when present at high levels. Metals can increase the synthesis of metallothioneins (MT), which bind free metal ions (Langston *et al.* 1998) to form an inactive metal–MT complex and therefore these proteins are capable of detoxifying the metals inside the cells (Park *et al.* 2001). The accumulation of metals also enhances the production of highly toxic radical oxygen species (ROS) (Fridovich 1998), which include the superoxide anion radical ($O_2^{-\bullet}$), hydrogen peroxide (H_2O_2) and the highly reactive hydroxyl radical ($OH^\bullet$), peroxyl radicals ($ROO^\bullet$), alkoxyl radicals ($RO^\bullet$) and peroxynitrite (HO-ONO) (Darley-Usmar *et al.* 1995). Hydrogen sulphide, known to be a potent inhibitor of antioxidant enzymes, reacts spontaneously with oxygen to generate many toxic oxygen and sulphide compounds, which in turn are capable of inflicting DNA damage (Pruski & Dixon 2003). Aerobic organisms possess a baseline status of antioxidant systems, involved in a variety of detoxification reactions, to assure the maintenance of a balance between production and removal of endogenous ROS and other pro-oxidants.

This pro-oxidant/antioxidant balance and detoxification of potentially damaging ROS is crucial for cellular homeostasis (Winston & Di Giulio 1991; Lemaire & Livingstone 1993; Livingstone 2001). The activities of antioxidant enzymes were described for some hydrothermal vent species, mainly in the mussels *Bathymodiolus azoricus* from MAR vent fields (Bebianno *et al.* 2005), in the tubeworm *Riftia pachyptila* and in the clam *Calyptogena magnifica* from the East Pacific Rise vent fields (Blum & Fridovich 1984).

Nevertheless, there is still a lack of information about the antioxidant defence systems in other hydrothermal species and their relation with environmental characteristics. Therefore, the aim of this study was to address several questions regarding the metal detoxification processes in both hydrothermal and costal shrimps, namely:

1 Are MT concentrations more similar in shrimps from the same environments? Is there any relationship between MT levels and antioxidant enzyme activities?

2 Is there a relation between the metabolic responses towards metals in shrimps from different environments?

3 Can these responses be due to specific environmental parameters related to microhabitat, or to inter-specific characteristics like feeding strategies?

To answer these questions we studied the adaptation strategies towards metals, especially those regarding MT levels and activities of antioxidant enzymes in two hydrothermal vent shrimp species (*M. fortunata* and *R. exoculata*) from the Rainbow vent field. We compared the results with two euryhaline coastal shrimp species (*Palaemon elegans*, Rathke 1837 and *Palaemonetes varians*, Leach 1814), with analogous microhabitat and feeding habits, *i.e.* detritivores (FAO – Food and Agriculture Organization of the United Nations 1980) collected in a lagoon system (Ria Formosa).

Material and Methods

Two hydrothermal vent shrimp species, *Rimicaris exoculata* (56.89 ± 7.32 mm carapace length, n = 8) and *Mirocaris fortunata* (21.89 ± 2.06 mm carapace length, n = 8) were collected from the Rainbow vent site, located on the Mid-Atlantic Ridge (MAR) (36°13′ N; 33°54.1′ W, 2500 m) (Fig. 1A), using the remote operated vehicle VICTOR6000 during the SEAHMA I cruise. Additionally, two coastal shrimp species, *Palaemon elegans* (36.29 ± 4.18 mm carapace length, n = 8) and *Palaemonetes varians* (33.47 ± 2.21 mm carapace length, n = 8), were collected from the margin of the Ria Formosa lagoon system in south Portugal (37°03′ N; 07°47′ W) (Fig. 1B) with a sub-superficial tow using a shrimp net (*c.* 40 cm diameter). The two coastal shrimp species were sampled at the same local site. The physical–chemical
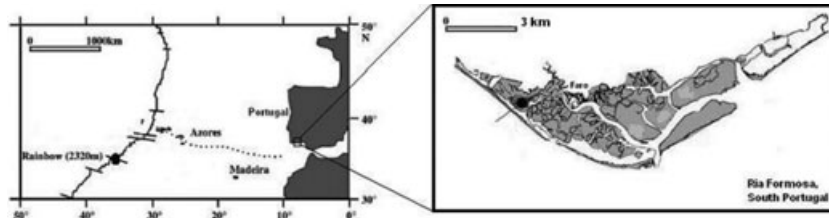
Fig. 1. Location of Rainbow hydrothermal vent site in the Azores Triple Junction area (A) and Ramalhete channel in the Ria Formosa lagoon (South Portugal) (B) (adapted from Caetano et al. 2002; Santos et al. 2004; Bebianno et al. 2005).

comparison between the two sampling sites is presented in Table 1. Both vent and coastal shrimp species were immediately frozen in liquid nitrogen after collection and stored at −80 °C until biochemical analysis. All dissected shrimp exoskeletons and gills were separated from soft tissues.

Metallothioneins

To determine the MT concentrations, the whole soft tissues of hydrothermal and coastal shrimps were homogenized in three volumes of 0.02 M TRIS-HCl buffer (pH 8.6) in an ice bath (4 °C). An aliquot of the homogenate (3 ml) was centrifuged at 30,000 g for 1 h at 4 °C. The supernatant (cytosol) was separated from the residual fraction, heat-treated at 80 °C for 10 min to precipitate the high molecular weight ligands, and subsequently centrifuged under the conditions described above. Aliquots of the heat-treated cytosol were used for the quantifica-tion of MT concentrations by differential pulse polarogra-phy according to the method described by Bebianno & Langston (1989). MT levels are expressed as mg·g^{-1} total protein concentrations.

Antioxidant enzymes

Antioxidant enzymatic activities were determined in the different shrimp species' edible tissues, after homogeniza-tion in 20 mM Tris buffer, pH 7.6, containing 1 mM of EDTA, 0.5 M of saccharose, 0.15 M of KCl and 1 mM of DTT. The homogenates were centrifuged at 500 g for 15 min at 4 °C to precipitate large particles and centri-fuged again at 12,000 g for 45 min at 4 °C to precipitate the mitochondrial fraction. Supernatants were purified on a Sephadex G-25 gel column to remove low molecular weight proteins.

Superoxide dismutase (SOD) activity (EC 1.15.1.1) was determined by measuring the reduction of cytochrome c by the xanthine oxidase/hypoxanthine system at 550 nm (McCord & Fridovich 1969). One unit of SOD is defined as the amount of enzyme that inhibits the reduction of cytochrome c by 50%. SOD activity is expressed in U SOD mg^{-1} total protein concentrations.

Catalase (CAT) activity (EC 1.11.1.6) was determined according to Greenwald (1985) by the decrease in absorb-ance at 240 nm because of H_2O_2 consumption. The CAT activity is expressed as mmoles min^{-1} mg^{-1} of total pro-tein concentrations.

Glutathione peroxidase activities were measured fol-lowing NADPH oxidation at 340 nm in the presence of excess glutathione reductase, reduced glutathione and corresponding peroxide (Lawrence & Burk 1976). The selenium-dependent glutathione peroxidase (Se-GPx) (EC 1.11.1.9) and total glutathione peroxidase (GPx) activities were measured by using respectively, H_2O_2 and cumene hydroperoxide as substrates. GPx activities are expressed as μmoles min^{-1} mg^{-1} of total protein concen-trations.

Table 1. Temperature, pH and concentration of chemical species in the end-member fluids of lagoon system Ria Formosa (South Portugal) and MAR vent field (Rainbow) compared with average seawater (adapted from Caetano et al. 1997; Douville et al. 2002).

Site	Ria Formosa 37°03′ N; 07°47′ W	Rainbow 36°13′ N, 33°54′ W	Seawater
T (°C)	17.3[a]	365[c]	–
pH	8.28[a]	2.8[c]	7.8
H$_2$S (mM)	–	1.0[c]	~0
CO$_2$(mM)	–	< 16[c]	–
CH$_4$(mM)	–	2.2–2.5[c]	~0
Cd (nM)	0.9 – 4.5[a]	130[c]	0.7
Cu (μM)	0.02 – 0.05[a]	140[c]	0.0033
Zn (μM)	0.02 – 0.03[a]	160[c]	0.028
Fe (μM)	8 – 52[b]	24000[c]	0.0045
Mn (μM)	2.5 – 6.3[b]	2250[c]	0.0013
Cl (mM)	–	750[c]	546
Co (μM)	–	13[c]	<2
Ag (nM)	–	47[c]	0.023
Ni (μM)	–	3[c]	<2
Si (mM)	–	6.9[c]	<0.2

[a]Instituto Hidrográfico (1998).
[b]Caetano et al. (1997).
[c]Douville et al. (2002).

Total protein concentrations

The whole edible tissues of vent and coastal shrimp were homogenized in 20 mM Tris buffer, pH 8.6, containing

150 mM of NaCl. The homogenates were centrifuged for 30 min at 30,000 g at 4 °C. Total protein concentrations were measured on supernatants by the Lowry method (Lowry *et al.* 1951) using BSA as reference standard material. Protein concentrations are expressed as mg·g^{-1} wet weight tissue.

The variability of MT concentrations and antioxidant enzymes activities was tested in the different species through the analysis of variance (one way-ANOVA). A Duncan test was used to determine significant differences between species for each variable. Regression analyses were also applied to assess the relationship between the concentrations of MT and antioxidant enzymes. A significance level of 0.05 was used for all statistical analysis, *i.e.* probability of P ≤ 0.05 was considered significant.

Results

In the hydrothermal vent shrimp from Rainbow, MT levels in *Rimicaris exoculata* (7.30 ± 0.66 mg·g^{-1} ww protein) were approximately sixfold higher compared with those found in *Mirocaris fortunata* (1.27 ± 0.27 mg·g^{-1} ww protein) ($p < 0.05$) (Fig. 2), whereas MT concentrations in *Palaemon elegans* were approximately 2.5-fold higher than in *Palaemonetes varians* (P < 0.05) (4.34 ± 0.99 mg·g^{-1} ww protein and 1.65 ± 0.39 mg·g^{-1} ww protein, respectively) (Fig. 2) and were not significantly different from *M. fortunata*. These results do not support the theory that MT concentrations are directly related to the environment where the shrimps were collected. Thus, MT concentrations followed the order: *R. exoculata* > *P. elegans* > *M. fortunata* = *P. varians*.
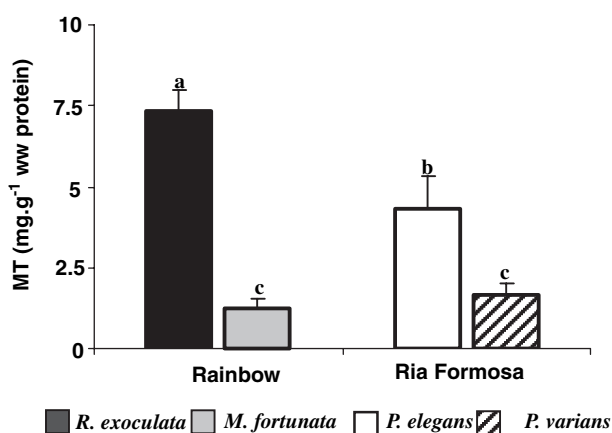

Fig. 2. Metallothionein concentrations (MT) in the edible tissues of hydrothermal (*Rimicaris exoculata* and *Mirocaris fortunata*) and coastal shrimp (*Palaemon elegans* and *Palaemonetes varians*). The data represent average ± standard deviation (SD), n = 16. Values followed by the same letter are not statistically different ($p > 0.05$).

Nevertheless, the higher MT levels in *R. exoculata* suggest that this shrimp species is more exposed to metal-contamination.

Regarding antioxidant enzymes activities, all the results obtained, except the ones for cytosolic CAT activity, show a negative relationship with MT levels, (MT = −0.345 SOD + 6.2, r = 0.728, P < 0.05; MT = −175.0 total GPx + 7.5, r = 0.858, P < 0.05; MT = −1344.8 Se-GPx + 11.8, r = 0.911, P < 0.05). The cytosolic SOD activity was significantly different among all sampled shrimp species (ANOVA, $F_{3,30} = 55.89$, P < 0.001). Cytosolic SOD activity was significantly higher in *M. fortunata* from Rainbow (1615.99 ± 5.66 U mg^{-1} protein) compared with the other vent and coastal species ($p < 0.05$). At the same time, the hydrothermal vent shrimp *R. exoculata* exhibited the lowest SOD activity (2.56 ± 0.66 U mg^{-1} protein) (Fig. 3A). No significant differences in the activity of cytosolic SOD were found between the two coastal shrimp species, *P. elegans* and *P. varians*, from the Ria Formosa Lagoon (P > 0.05) (5.14 ± 1.58 and 5.67 ± 1.73 U mg^{-1} protein, respectively) (Fig. 3A).

All shrimp species had significantly different cytosolic CAT activity (ANOVA, $F_{3,26} = 28.60$, P < 0.001). The activity of cytosolic CAT was approximately threefold higher in the two vent shrimp species (0.0042 ± 0.0005 mmoles min^{-1} mg^{-1} protein for *R. exoculata* and 0.0048 ± 0.001 mmoles min^{-1} mg^{-1} protein for *M. fortunata*) compared with their coastal counterparts (0.0014 ± 0.0005 mmoles min^{-1} mg^{-1} protein for *P. elegans* and 0.002 ± 0.0005 mmoles min^{-1} mg^{-1} protein for *P. varians*) (P > 0.05) (Fig. 3B). Each and every analysed shrimp species was significantly different for total GPx activity (ANOVA, $F_{3,26} = 18.47$, P < 0.001). The antioxidant enzyme levels followed a similar pattern of cytosolic SOD, where a significantly higher activity was observed in *M. fortunata* (0.040 ± 0.01 μmoles min^{-1} mg^{-1} protein) compared with all the other shrimp species ($p < 0.05$) (Fig. 3C). As occurred for SOD and CAT activities, no significant differences were observed in total GPx between coastal shrimp *P. elegans* (0.023 ± 0.004 μmoles min^{-1} mg^{-1} protein) and *P. varians* (0.015 ± 0.007 μmoles min^{-1} mg^{-1} protein) collected in the Ria Formosa Lagoon ($p > 0.05$). Moreover, the hydrothermal vent shrimp *R. exoculata* exhibited no significant differences compared with *P. varians* (P > 0.05) (Fig. 3C). As occurred for all above antioxidant enzymes, Se-GPx activity was significantly different for all shrimp species (ANOVA, $F_{3,27} = 4.32$, P < 0.01). This enzyme activity represents approximately one third of the total GPx activity in both hydrothermal and coastal shrimp species (Fig. 3D). No significant differences were found in GPx activities between the hydrothermal shrimp *M. fortunata*
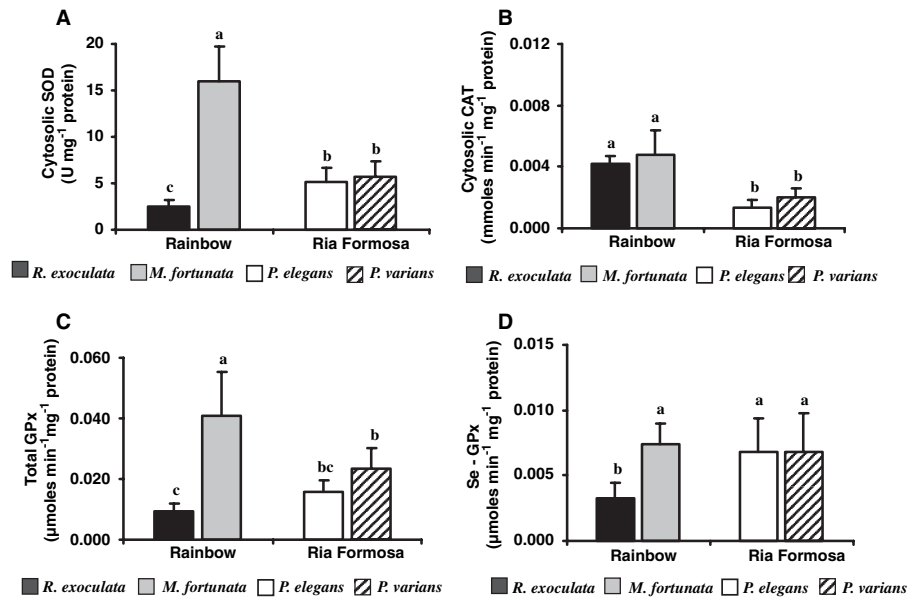
Fig. 3. Antioxidant enzymes activities of (A) cytosolic superoxide dismutase; (B) cytosolic catalase; (C) Total glutathione peroxidase and (D) selenium-dependent glutathione peroxidase in edible tissues of hydrothermal (*Rimicaris exoculata* and *Mirocaris fortunata*) and coastal shrimp (*Palaemon elegans* and *Palaemonetes varians*). The data represent average and ± standard deviation (SD) for n = 16. Values followed by the same letter are not statistically different ($p > 0.05$).

$(0.007 \pm 0.001$ μmoles min^{-1} mg^{-1} protein) and both coastal species from Ria Formosa ($p > 0.05$). On the other hand, Se-GPx activity in *R. exoculata* $(0.003 \pm 0.001$ min^{-1} mg^{-1} protein) was approximately half of that observed for the other vent and coastal species ($p < 0.05$) (Fig. 3D).

As occurred for MT levels, no direct relationships were found in antioxidant enzyme activities between the two shrimp species from Rainbow site; however, their coastal counterparts do not show significant differences between them. Direct correlation with environment was only found in cytosolic CAT activity, but there were no significant differences between shrimp species within hydrothermal vent and coastal environments.

Discussion

An intriguing vent paradox is how to reconcile the fast growth rates and abundant biomass that typify vent species with the highly toxic and stressful nature of their deep-sea environment (Dixon *et al.* 2000). This is particularly evident at the Rainbow hydrothermal vent site, where the highest metal concentrations in MAR hydrothermal area can be found (Douville *et al.* 1997, 2002; Desbruyères *et al.* 2000) and caridean shrimp species *Rimicaris exoculata* and *Mirocaris fortunata* together with the vent mussel *Bathymodiolus azoricus* co-dominate the Rainbow hydrothermal vent megafauna.

Metallothioneins have been proposed as a biomarker of metallic exposure in several organisms (Amiard & Cosson 1997). Amiard *et al.* (2006) recently compiled several studies showing a clear correlation between metallic concentrations with MT levels, and an evident induction of this protein after Cd, Cu and Zn exposures in aquatic invertebrates, including decapod shrimps. Crustacean species are widely used as biological indicators of environmental alterations, as they play a key ecological role as planktivorous grazers, epibenthic scavengers or as prey species (Clark 1989). Generally, these studies are focussed mainly on the hepatopancreas tissue as it has a central role in the metabolism, storage and detoxification of metals (Pourang *et al.* 2004). In the present work, however, we considered the whole soft tissue due to technical constraints for antioxidant enzyme determination.

As antioxidant enzymes can also protect against metal-induced reactive oxygen species, it is important to understand both MT and antioxidant enzymatic responses in these organisms. Therefore, this study was the first attempt to compare MT levels and antioxidant defence systems in four shrimp species from hydrothermal vent and coastal environments and try to explain the importance of such responses in the resistance and tolerance of these species to a metal-rich environment.

Considering the possible influence of the environment in MT concentrations, the results obtained showed that MT levels were markedly different between shrimp species

from each vent and coastal site. We expected a higher similarity in MT concentrations between shrimp from the same type of environment, as the Rainbow shrimp exhibited higher metal concentration levels in their fluids and in whole body tissue burden (Kádár *et al.* 2006 obtained for *Rimicaris*: 35.6×10^3 $\mu g \cdot g^{-1}$ dry weight Fe, 1.8×10^3 $\mu g \cdot g^{-1}$ dry weight Zn, 0.8×10^3 $\mu g \cdot g^{-1}$ dry weight Cu and for *Mirocaris*: 6.6×10^3 $\mu g \cdot g^{-1}$ dry weight Fe, 2.5×10^3 $\mu g \cdot g^{-1}$ dry weight Zn, 1.0×10^3 $\mu g \cdot g^{-1}$ dry weight Cu) when compared with the coastal species collected in the Ria Formosa Lagoon (data not shown). However, this was only true for *R. exoculata*, while the other vent shrimp, *M. fortunata*, had MT concentrations similar to those found for the coastal species *Palaemon elegans*. Although *M. fortunata* are found more distant from active venting than *R. exoculata*, and therefore have a lower exposure to the vent fluids, they seem to accumulate more metals in their tissues, which may suggest more efficient detoxification strategies to this potentially toxic environment (Kádár *et al.* 2006).

Therefore, the differences observed in MT levels between vent and coastal shrimp can derive from interspecific differences in the basal levels of these proteins, rather than reflecting a metabolic response to their environments. Geret *et al.* 2002 found similar MT levels in *R. exoculata* from Rainbow hydrothermal field. However, no information concerning the basal MT levels in *M. fortunata*, *P. elegans* and *Palaemonetes varians* is available. Also, in crustaceans a relatively high amount of metals is associated with the insoluble forms (Geret *et al.* 2002) that can be mobilized and immobilized during the moult cycle (Engel & Brouwer 1991, 1993). In hydrothermal vent shrimp, intra-specific adaptations to deep-sea hydrothermal conditions can also derive from their different nutritional behaviours, *i.e. M. fortunata* has been described as an opportunistic scavenger while *R. exoculata* possess symbiotic bacteria in their branchial chambers (Gebruk *et al.* 2000). Nevertheless, we can also hypothesize that, although coastal shrimp exhibit the same sampling environment and analogous feeding habits, vent shrimp have different microhabitats (described earlier). Unfortunately no available data concerning metal concentration levels in the surrounding water of each microhabitat were found in the literature to confirm this assumption.

In general, the antioxidant enzyme activities in the two hydrothermal shrimp species are significantly lower than those found for the mussel *B. azoricus* from the same hydrothermal vent site, except the cytosolic SOD activity (5.52 ± 1.08 $U \cdot mg^{-1}$ protein), which was the same order of magnitude (Bebianno *et al.* 2005). Hydrothermal vent mussel species *B. azoricus* at Rainbow site exhibit much higher cytosolic CAT, total GPx and Se-GPx activities. However, cytosolic SOD activity (5.52 ± 1.08 $U \cdot mg^{-1}$

protein) seems to be in agreement with that obtained in shrimp species, although being closer to coastal shrimp species rather than hydrothermal vent shrimp species.

Concerning the relationship between MT levels and antioxidant enzymes, results point out that in general, antioxidant enzyme activities (especially cytosolic SOD, Total GPx and Se-GPx) in both vent and coastal shrimp species had an inverse pattern compared with the MT levels, suggesting a negative relationship between these two protection systems. However, this negative relationship is more noticeable among vent shrimp species. Although antioxidant enzymes are the main factor responsible for ROS detoxification inside the cells, the antioxidant properties of MT have also been described, mainly in the elimination of the hydroxyl radical (Chubatsu & Meneghini 1993). This suggests that when MT levels in vent and coastal shrimp are enhanced, they are more efficiently sequestered from the intracellular medium. Consequently, metal-induced reactive oxygen species are less likely to be formed when MT synthesis increases, leading to a natural decrease in the antioxidant enzymatic protections.

Even so, the biochemical responses towards metals in coastal shrimp are more similar between them, than between hydrothermal vent shrimp. Thus, microhabitat and feeding habitats are the crucial variables for metal uptake and consequently will influence the metal detoxification systems.

Summary

Very few studies deal with the specific biochemical responses from hydrothermal vent organisms as an adaptation to their extreme environment. Shrimp are key species in these environments as they dominate the hydrothermal vent fauna along with hydrothermal vent mussels of the genus *Bathymodiolus*. Results obtained suggest that biochemical responses in vent and coastal shrimp are not only affected by environmental characteristics but also by interspecific differences. The detoxification strategies towards metals (MT and antioxidant enzymes) observed in several shrimp species suggest distinct metabolic responses; nevertheless these responses confer successful adaptations to survival in a metal-extreme environment.

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