

The crustacean selenoproteome similarity to other arthropods homologs: A mini review

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Abstract Selenoproteins (Sels) are involved in oxidative stress regulation. Glutathione peroxidase (GPx) and thioredoxin reductase are among the most studied Sels in crustaceans. Since their expressions and activities are affected by pathogens, environmental and metabolic factors, their functions might be key factors to orchestrate the redox cellular balance. The most studied invertebrate selenoproteome is from *Drosophila*. In this fly, SelD and SelB are involved in selenoproteins synthesis, whereas SelBthD, SelH and SelK are associated with embryogenesis and animal viability. None of the Sels found in *Drosophila* have been identified in marine crustaceans yet, and their discovery and function identification is an interesting research challenge. SelM has been identified in crustaceans and is differentially expressed in tissues, while its function remains to be clarified. SelW and G-rich Sel were recently discovered in marine crustaceans and their functions are yet to be clearly defined. To fully understand the crustacean selenoproteome, it is still necessary to identify important Sels such as the SelD, SelBthD and SelB homologs. This knowledge can also be useful for marine crustacean industry to propose better culture strategies, enhanced health and improved profits.

Keywords: functions, invertebrates, redox, selenoproteins

INTRODUCTION

Modulation of reactive oxygen species (ROS) plays a key role in metabolism (Alsina et al. 1996). All known organisms have specialized antioxidant enzymes to manage oxidative stress. Selenoproteins (Sels) are proteins that contain selenocysteine (Sec), a modified cysteine residue in which S is replaced by Se, are involved in the regulation of cellular redox balance. The selective advantage of selenoenzymes compared to cysteine or serine containing enzymes is their broad range of substrates and their activity under a wide range of micro-environmental conditions (Gromer et al. 2003). Peroxidases are antioxidant enzymes that catalyze the reduction of peroxide (H₂O₂) or hydroperoxides using a donor substrate that is oxidized, regulating H₂O₂ levels. The selenocysteine tRNA (*tRNA*^{Sec}) synthetase and selenophosphate synthetase (*sps1* and *sps2*) genes have been identified in *Drosophila melanogaster* (Alsina et al. 1996; Alsina et al. 1998). Selenophosphate synthetase or SelD, an enzyme required for synthesis of Sels is the most studied Sel. Although the *Drosophila* Sels have been isolated and characterized, and it is thought that they are present in the cytoplasm, it is not clear whether this is their final cellular localization. The so far known invertebrate Sels have been found in insects (Martín-Romero et al. 2001), crustaceans (Clavero-Salas et al. 2007), porifera (Müller et al. 2005) and cnidaria (Bode et al. 2002). Insect Sels have been a useful tool to study H₂O₂ function and degradation because of their high affinity for this ROS and *Drosophila* availability as a model organism. SelD and SelBthD from *Drosophila* have been well characterized. SelD homologs have been identified in *P. monodon* (Preechaphol et al. 2010) and in the rotifer *Brachionus plicatilis* (Clark et al. 2012). Selenoprotein M (SelM) was identified in a crab (Müller et al. 2005) and a marine shrimp (Clavero-Salas et al. 2007), indicating that perhaps the presence of different Sels extends also to marine

invertebrates, but their physiological roles are only beginning to be studied. In this article, we review the current knowledge about invertebrate Sels, with special emphasis in the search for these proteins in marine invertebrates.

Stress related Sels with peroxidase activity: Glutathione peroxidase and thioredoxin reductase

One of the most studied Sels in marine invertebrates is glutathione peroxidase (GPx). GPx belongs to an enzyme family with peroxidase activity. They are 84 kDa, homotetrameric (GPx1, GPx2 and GPx3) or monomeric (GPx4) proteins containing one selenocysteine per monomer unit. Selenocysteine is key for the enzyme function. In the cladoceran *Daphnia magna* GPx has been studied as a biomarker and contaminant response enzyme. Comparative analyses of selenoprotein-rich and -deficient organisms revealed that aquatic organisms generally have large selenoproteomes, whereas several groups of terrestrial organisms appear to have reduced their selenoproteomes (Lobanov et al. 2006). GPx appears to be among the most responsive of the induced biomarkers of oxidative stress in *D. magna* exposed to sub lethal levels of menadione, paraquat, endosulfan, cadmium and copper for 48 hrs. This suggests that GPx is important to detoxify the H₂O₂ produced in response to the xenobiotics studied (Barata et al. 2005b). In contrast, significant decrease of *D. magna* GPx activity was found in organisms exposed to N-heterocyclic polycyclic aromatic hydrocarbons (N-PAHs), such as phenanthrene and 1,10-phenanthroline (Feldmannová et al. 2006), indicating that GPx antioxidant response could be inhibited by these aromatic hydrocarbons. Therefore *D. magna* GPx activity responds to different stresses depending on the type of molecules involved. It appears that when the antioxidant response is overwhelmed, GPx activity decreases or ceases. The same seems to occur in the crustacean, *Artemia parthenogenetica*. The therapeutic agents clofibrate and clofibric acid in *A. parthenogenetica* were responsible for significant decreases in GPx activity (Nunes et al. 2006). GPx is also involved in aging in *D. magna*, where aging was accompanied by selective loss of key antioxidant enzymes, including GPx, and age-related increases in lipid peroxides were at least partially due to the functional imbalance of enzymatic antioxidant defences as GPx (Barata et al. 2005a).

In crabs, GPx activity has been studied in response to different contaminants. In the blue crab *Callinectes sapidus* copper exposure leads to increased activity of GPx (Brouwer and Brouwer, 1998). In *Parasesarma erythodactyla* GPx was higher in individuals where Pb, Cu, Cr, Zn, Cd, As and Se were elevated. Therefore, GPx may be a sensitive biomarker of metal exposure and a secondary marker when accumulated metals are high (MacFarlane et al. 2006). In gills and hepatopancreas of the portunid crab *Charybdis japonica* exposed to Cd, higher GPx was detected as soon as 0.5 days, increased continuously and was later reduced, but still, it was maintained at higher concentration than in unexposed animals, even after 15 days of exposure. Gills were more sensitive to Cd than hepatopancreas, although hepatopancreas was the main detoxification tissue for ROS (Pan and Zhang, 2006). In the marine crab *Scylla serrata* naphthalene decreased GPx activity in hepatopancreas and haemolymph (Vijayavel et al. 2004) and a 30 day sub lethal effect decreased GPx activity in the gonads (Vijayavel et al. 2005). In the crab *Carcinus maenas*, hepatopancreas connective tissue and the apex of duct cells were immunostained with GPx antibodies (Orbea et al. 2000), until now there is no report on GPx activity in response to stress in *C. maenas*. It seems that crabs GPx respond to contaminants in a short period of time, but in response to long-term stress, GPx activity decreased. Lab-acclimated adult male grass shrimp *Palaemonetes pugio* responded similarly. Shrimps were exposed to empirically calculated 96-hrs male-specific LC₅₀ concentrations of fipronil (FP, a phenylpyrazole GABA disrupting pesticide), endosulfan (ES, a cyclodiene GABA disrupting pesticide), or Cd, as well as a control. GPx was significantly up-regulated by all these three treatments (Griffitt et al. 2006).

GPx has also been studied in freshwater prawns and crayfish. In the freshwater prawn *Macrobrachium rosenbergii* fed a diet supplemented with vitamin E, lipid peroxidation was inhibited in hepatopancreas and gills. In these animals, GPx activity was significantly elevated in hepatopancreas but its activity remained unaltered in gills (Dandapat et al. 2000). These results suggest that other proteins besides GPx are involved in gill and muscle antioxidant response and that vitamin E does not substitute the antioxidant activity derived from Se dependent antioxidant proteins. During early larval development and metamorphosis *M. rosenbergii* appears to provoke high oxidative stress as suggested by high content of thiobarbituric acid reactive substances (TBARS). This may be due to direct exposure of the larvae to ambient oxygen in the water as well as their low antioxidant potential. As GPx did not exhibit specific pattern of changes in *M. rosenbergii* larval development (Dandapat et al. 2003), it is argued that some other antioxidant proteins are involved in H₂O₂ regulation as second messenger. A selenium dependent GPx cDNA was originally cloned from *M. rosenbergii* haemocytes and later detected in

haemocytes, hepatopancreas, muscle, stomach, gill, intestine, eyestalk, heart, epidermis, lymph organ, ventral nerve cord, testis and ovary, indicating the broad cellular distribution of this protein. *M. rosenbergii* up-regulation of GPx activity and mRNA transcripts were involved with the protection against injection with the pathogen *Debaryomyces hansenii* (Yeh et al. 2009). Both results indicate that GPx has an important function in H₂O₂ regulation in different tissues and in response to pathogens.

Several studies have investigated GPx activity in response to pathogens. In the shrimp *Palaemonetes argentinus* infected with the gill chamber parasite *Probopyrus ringueleti*, known for its capacity to cause host metabolic changes, including changes in oxygen consumption rates, no significant differences were detected in GPx activity (Neves et al. 2000). Most of the white spot syndrome virus (WSSV)-infected shrimps had GPx decreased activity after the infection. In *Fenneropenaeus indicus*, a significant reduction in the activity of GPx was detected in WSSV-infected shrimps compared to uninfected animals (Mohankumar and Ramasamy, 2006). Another example is the significant decrease of GPx activity in *Penaeus monodon* after WSSV infection by intramuscular injection (Mathew et al. 2007). However, WSSV-resistant *Penaeus japonicus* had higher GPx expression, suggesting that antioxidants are essential components participating in the antiviral process (He et al. 2005). Bacteria effect on GPx activity in shrimp is variable. When *L. vannamei* was challenged with *Vibrio harveyi*, GPx was substantially down-regulated, indicating that this may lead to accumulation of H₂O₂ to mount the attack to the pathogen (Wang et al. 2010). In contrast, when *L. vannamei* was fed with the probiotic *Bacillus subtilis* E20, an increase in survival rate was detected but no significant differences were found in GPx activity and, in that case, the increased resistance was shown to be mediated by immune modifications in phenoloxidase activity, phagocytic activity and clearance efficiency (Tseng et al. 2009). The responses appear to vary since *Pediococcus acidilactici* MA18/5M, used as prebiotic bacteria, significantly increased GPx activity and reduced the susceptibility of *Litopenaeus stylirostris* to the pathogen *Vibrio nigripulchritudo* (Castex et al. 2009). Besides responding to the host and pathogen species, GPx activity is also regulated by the diet and the environment. An example of diet regulation is the white shrimp *L. vannamei* fed a diet containing 2.0 g kg⁻¹ sodium alginate that induced a significant decrease in GPx activity, but an increase in phagocytic activity.

The shrimp fed a diet containing sodium alginate at 0.5, 1.0 or 2.0 g kg⁻¹ had increased clearance efficiency of *Vibrio alginolyticus* (Cheng et al. 2005), suggesting that other H₂O₂ hydrolases are involved in increased immune resistance to *V. alginolyticus* infection. Conversely, the respiratory bursts of *L. vannamei* not fed with sodium alginate, increased significantly after a *V. alginolyticus* injection to kill the pathogen, and then induced the increase in GPx activity to protect cells against oxidative damage. However, GPx activity increased as a result of up-regulated expression of GPx mRNA which was induced by the increase in H₂O₂ (Liu et al. 2007).

A selenium-dependent GPx has been cloned from *F. chinensis*. The alignment of the deduced GPx amino acid sequences with homologous proteins from other species showed that the essential residues for enzyme activity are highly conserved. RT-PCR analysis showed that the transcript of *F. chinensis* GPx increased in response to *Vibrio anguillarum* infection. GPx activity in gill tissues quickly increased at 6 hrs after *V. anguillarum* challenge and was maintained at relatively high levels from 6 to 24 hrs (Ren et al. 2009). The increase in GPx transcripts and activity in response to pathogens indicate that this Sel is an important enzyme in the oxidative burst response associated with an infection. Work associated with the increase in the aggressiveness of the oxidative bursts to the pathogens and the concomitant increase in antioxidant enzymes protection of the host is necessary in cultivable marine crustaceans.

In aquaculture conditions, especially at nursery stage, antibiotics are commonly used. Antibiotic molecules also influence the antioxidant metabolism in crustaceans. GPx is regulated by the antibiotic and antifungi saponin. GPx activity, phagocytic activity and clearance efficiency to *V. alginolyticus* in *L. vannamei* is enhanced by saponin (Su and Chen, 2008). The study of non-environmentally hazardous antimicrobials in the enhancement of oxidative burst against pathogens should be an actively field of crustacean mariculture research. Which antibiotics, antifungal and signal molecules are the more promising molecules in culture conditions for oxidative burst regulation?

Culture (pond) environment is crucial in the regulation of antioxidant enzymes like GPx. The available information on GPx and other Sels with peroxidase activity in cultivable marine crustaceans is still limited. In *L. vannamei*, acidic (5.6) or alkaline (9.3) pH induced oxidative stress and activated the expression of GPx (Wang et al. 2009). Work is still necessary to understand the effects of

environmental changes such as oxygen, temperature and salinity, as well as the marine crustaceans metabolic state including life stage, molting cycle, reproductive state, circadian and circannual state, stress conditions related to culture density on GPx expression and activity. A full length GPx transcript was sequenced in the penaeid shrimp *Metapenaeus ensis*, mRNA expression, studies provide insights on the regulation of ROS in the ovarian maturation process and the role of GPx in crustacean reproductive biology (Wu and Chu, 2010). The understanding of antioxidant Sels regulation such as GPx under environmental, pathogen and intrinsic related conditions may lead to better culture strategies which in turn result in higher production efficiency. Experimental designs like response surfaces are useful to understand the interaction of these factors and may help us to propose strategies to modulate enzyme antioxidant activity in the appropriate times to respond to pathogens and environmental disturbances for better defences and at the same time, minimize ROS- and reactive nitrogen species (RNS)-induced cellular damage.

Thioredoxin reductases (Trxr) is another group of important Sels. Mammalian Trxrs contain Sec. *Drosophila* has two Trxr, *Apis* sp. and *Anopheles* sp. have a single Trxr gene (Corona and Robinson, 2006). In *Drosophila*, *Trxr-1* encodes three splice variants that include one mitochondrial and two cytoplasmic forms (Missirlis et al. 2002). The functional significance of the second *Drosophila* Trxr gene (*Trxr2*) is unknown, but it encodes a protein with a potential mitochondrial targeting peptide. *Anopheles* sp. has a single Trxr gene, and, as in the *Drosophila* ortholog, has three splice variants coding for one mitochondrial and two cytoplasmic forms (Bauer et al. 2003). *Apis* also has a single Trxr gene. Full genome analysis revealed that, as in *D. melanogaster*, the enzyme glutathione reductase is absent in *Anopheles gambiae* and functionally substituted by the thioredoxin system (Bauer et al. 2003). Trxr was reported from the tsetse fly *Glossina morsitans morsitans* and showed a modulation of the expression during fly development, in different adult tissues, in the adult midgut through the digestive cycle and following trypanosome infection (Munks et al. 2005). A Trxr was reported from the Chinese mitten crab *Eriocheir sinensis*. Transcripts were identified in gills, gonad, hepatopancreas, muscle, heart and haemocytes. With *Listonella anguillarum* challenge, Trxr reached the maximum level at 6 hrs post-stimulation, and then dropped back to the original level gradually (Mu et al. 2009). Sel L, which is a Trxr like protein with double Sec residues, has an unusual occurrence in diverse aquatic organisms including the invertebrates *Homarus americanus* and *D. magna* (Shchedrina et al. 2007). A Trx was reported from *L. vannamei*, interestingly, this Trx contains besides the canonical active site CXXC disulfide motif, one Cys (C73) residue in the interface of a putative dimer previously reported for human Trx. It is mainly expressed in gills and pleopods and the variation of Trxr mRNA upon hypoxia and re-oxygenation is not statistically significant (Aispuro-Hernandez et al. 2008). Acidic (5.6) or alkaline (9.3) pH induces oxidative stress and activates the expression of Trx in *L. vannamei* (Wang et al. 2009). As some correlations have been observed in crustacean genes with respect to mammals, the question becomes, Is there another *L. vannamei* Trxr with Sec in the active site? Work has to be done to address this question.

***Drosophila* Selenoprotein D and B are involved in Selenoproteins synthesis pathway. Do marine crustaceans homologs exist?**

Sel synthesis has been well studied in bacteria and requires the participation of four gene products (Böck et al. 1991): selenocysteine synthase (*selA*), selenocysteine-specific elongation factor (*selB*), selenocysteine-specific tRNA (*selC*) and selenophosphate synthetase (*selD*), an enzyme required for Sels synthesis. As originally cloned in flies, the highly conserved *selD* gene has been identified as *sps1* (*selD* in flies) (Alsina et al. 1998). The *selD* gene also known as *patufet* gene (*ptuf*) was first studied by Alsina et al. (1998); this gene encodes the *Drosophila* homologue of selenophosphate synthetase (*sps1*) and is involved in Sel biosynthesis. Disruption of the *Drosophila selD* gene results in impairment of Sel biosynthesis, ROS burst and larval lethality (Alsina et al. 1998; Morey et al. 2003). Wild-type flies showed a highly dynamic pattern of *selD* mRNA expression during larval and pupal development (Alsina et al. 1999). Mutant organisms that have no Sel synthesis have lower levels of cell proliferation, increase the proportion of cells arrested in G2 and the levels of ROS. Those results suggested an important role of Sels in cell function and have shown a close correlation between *selD* expression with cell proliferation, the involvement of *selD* on the redox state of the cell and the effects of *selD* mutants on cell-cycle progression. All these effects are likely mediated through the synthesis and function of Sels. This supports a leading role for Sels in redox regulation and cell-cycle progression.

To study the function of these Sels in development and growth, a null mutation in the *D. melanogaster* (*selD*) gene *selD(ptuf)* was obtained (Serras et al. 2001). The *selD(ptuf)* loss-of-function mutation causes aberrant cell proliferation and differentiation patterns in the brain and imaginal discs, as

deduced from genetic mosaics, patterns of gene expression and analysis of cell cycle markers. Therefore, the use of *Drosophila* imaginal discs and brain and in particular the *selD(ptuf)* mutation, provides a good model to investigate the role of Sels in the regulation of cell proliferation, growth and differentiation. Nervous system development studies are very scarce in marine crustaceans; discovery and silencing of *selD* in marine crustaceans could lead to important knowledge on neuronal growth and development.

The alteration of the redox balance caused by *selD(ptuf)* mutation affects the Ras/MAPK signalling pathway (Morey et al. 2001). The *selD(ptuf)* mutation suppresses the phenotypes in the eye and the wing caused by hyper activation of the Ras/MAPK cassette. The mutation also suppresses the *Drosophila* EGF receptor (DER) and sevenless (Sev) receptor tyrosine kinases (RTKs), which signal in the eye and wing, respectively. No dominant interaction was observed with *selD(ptuf)* conditions in the Wnt, notch, insulin-Pi3K, and DPP signalling pathways. It seems that Sels selectively modulate the Ras/MAPK signalling pathway through their antioxidant function. This is further supported by the fact that a selenoprotein-independent increase in ROS caused by the catalase amorphic *Cat(n1)* allele also reduces Ras/MAPK signalling (Shim et al. 2009). They presented the first evidence for the role of intracellular redox environment in signalling pathways in *Drosophila* as a whole organism. SelD regulates the intracellular glutamine by inhibiting glutamine synthetase expression and glutamine in elevated levels works as an intracellular signal (Shim et al. 2009).

H₂O₂ is one of the most stable ROS and functions as a second messenger in signalling pathways. Certain Sels as GPx and Trx are involved in redox balance through their peroxidase activity. There are no crustacean reports of *selD* and it is very likely that crustacean Sels need synthesis accessory proteins as SelD. The identification and study of physiological role of SelD-like proteins in crustaceans and Sels synthesis will help in the development of new strategies for the improvement of their redox metabolism.

Incorporation of Sec into Sels requires several gene products, such as the specialized elongation factor SelB and the tRNA(Sec). While the molecular actors have been discovered and their role elucidated in the eubacterial machinery, the data pointed to a higher degree of complexity in archaea and eukaryotes (Fagegaltier et al. 2001). *Drosophila* SelB/eEFsec is not essential for viability, longevity or oxidative stress defence (Hirosawa-Takamori et al. 2004). The organisms lacking the SelB/eEFsec gene were viable and fertile and oxidative balance and the lifespan of these flies are not affected. Thus, Sels may have developed an insect-specific adoption of novel functions once the components of their redox regulating system became independent of Sels biosynthesis. The fact that Sels biosynthesis is maintained in flies suggests that following initial gene duplication events in ancestral organisms, Sels-coding genes may have adopted new and possibly important, but non-vital, functions. These processes may account for the continued requirement for Sels synthesis once the redox homeostasis system became independent of Sec-bearing enzymes during the course of insect evolution. No crustacean elongation factors as SelB have been discovered, nothing is known about the importance of Sels elongation factors in crustaceans redox homeostasis system and viability.

Embryogenesis related selenoproteins: BthD, H and K

In *Drosophila*, an *in silico* program that searches for Sec insertion sequence elements to detect Sels, followed by subsequent metabolic labeling with ⁷⁵Se and gene signature analyses, was used to detect Sel BthD (Martin-Romero et al. 2001). BthD is expressed dynamically during *Drosophila* development (Kwon et al. 2003). High levels are detected in the adult ovary, and a large maternal contribution of BthD protein and RNA is given to early embryos. At late stages of embryogenesis, BthD accumulates in the developing salivary gland. RNAi studies revealed that BthD is required for proper salivary gland morphogenesis and the loss of BthD reduced animal viability. Such an expression profile argues against BthD having a general function in cellular metabolism. In tissues where it is expressed, BthD is localized in the cytoplasm and is not detected in the nucleus. BthD staining in SL2 cells co-localizes with a known Golgi marker. It is tempting to speculate, therefore, that BthD protein traffics through the Golgi to another compartment.

SelK is a human and mouse Sel homologue of *D. melanogaster* G-rich (Martin-Romero et al. 2001). *dselH* and *dselK* genes, were identified in *D. melanogaster*. Thereby, *dselK* is homologue to G-rich. Subcellular localization analysis using GFP-tagged G-rich showed that G-rich was localized in the Golgi apparatus. The fusion protein was co-localized with the Golgi marker proteins but not with

endoplasmic reticulum (ER) (Chen et al. 2006). RNAi was used in *D. melanogaster* embryos and in Schneider S2 cells to inhibit expression of dselH and dselK. The inhibition of either dselH or dselK expression significantly reduces viability in embryos. dselH silencing decreases total antioxidant capacity in embryos and Schneider cells, and increases lipid peroxidation in cells. These studies suggest that the well-known role of Sels in vertebrate antioxidant defences also extends to include invertebrates (Morozova et al. 2003). No BthD, dselH or dselK homologs have been identified in crustaceans. Nothing is known about Sels role in crustacean embryogenesis, improvement of Sels-dependent redox signalling pathways and metabolism may lead to the increase of larvae viability and survival rate.

Crustacean tissue differentially expressed selenoprotein: Selenoprotein M

The first marine invertebrate SelM identified was from *Suberites domuncula* (porifera) (Müller et al. 2005). Using differential display of transcripts, they demonstrated that, after a 72-hrs exposure of primmorphs to selenium, a gene coding for SelM was expressed. The deduced protein sequence of SelM (14 kDa) shows characteristic features of metazoan Sels. The catalytic site of *S. domuncula* SelM, Ser-Gly-Sel-Arg-Leu, is similar to the human Gly-Gly-Sel-Gln-Leu. The complete protein, with a calculated molecular mass of 13.9 kDa (123-amino-acid ORF) shares the highest sequence similarity with the 15 kDa SelM from humans (accession number NP_536355M) (Korotkov et al. 2002); and it has comparatively low similarity to the *D. melanogaster* putative protein. Therefore, the sponge molecule was termed selenoprotein M (SelM_SUBDO) and its cDNA *SDSelM*. We isolated a *SelM* cDNA from *L. vannamei* (Clavero-Salas et al. 2007). *SelM* was found to be homologous to human SelM (Gromer et al. 2005), *Ixodes scapularis* SelM (Ribeiro et al. 2006) and *Tribolium castaneum* SelM (GenBank accession XM_965244) suggesting a wide distribution of SelM. Expression in the gill of shrimp infected with WSSV was transiently reduced at 1, 3 and 12 hrs post-infection and increased at 6 and 24 hrs (Clavero-Salas et al. 2007). This modulation is interesting and prompts its possible involvement in alleviating the oxidative stress caused by WSSV-infection. We also demonstrated that SelM was detected in gills, muscle, hepatopancreas and pleopods, with higher abundance in the hepatopancreas and gills. Peroxidase activity decreased upon silencing of SelM in gills, but no significant effect was detected in hepatopancreas. In contrast, total cell H₂O₂ concentration did not change in gills and hepatopancreas of silenced shrimp (García-Triana et al. 2010). The difference in expression during a disease and in different tissues indicates that SelM is involved in diverse regulatory responses. Which tissue-specific function is performed by SelM? Is SelM involved in H₂O₂ regulation as a second messenger in the different tissues? Is this function different during pathogens response?

Unknown function selenoprotein: Selenoprotein W

Selenoprotein W (SelW) is a small selenoprotein (85 to 88 amino acids) identified in different vertebrates, such as mice, rats, monkeys, humans, sheep, pigs, fish and chickens. The biological function of SelW has not been definitely identified. Evidence has been obtained that it can serve as an antioxidant, in response to stress, in cell immunity, as specific target for methyl mercury, and has a thioredoxin-like function (Whanger, 2009). In marine crustaceans, SelW has only been reported in *P. monodon*, where yellow head virus (YHV) infected *P. monodon* showed a decreased expression of SelW (Chintapitaksakul et al. 2008), and we also have a small cDNA sequence for SelW in the shrimp *L. vannamei* (Yepiz-Plascencia et al. unpublished data), but experiments to address its functions have not done yet. Do SelW and other novel Sels have the same functions as the vertebrate counterparts currently known? As SelW, it is possible that other Sels will be discovered and their metabolic roles must be elucidated to completely understand the selenoproteome function in marine crustaceans metabolism.

Novel selenoproteins studies in marine crustaceans

Figure 1 shows a dendrogram obtained with data available in GenBank for a conserved region of Sels sequences from invertebrates and two Trxr of *D. melanogaster*. Sels synthesis involves closely related proteins, *Drosophila* Sps2 is more related to *L. major*, *T. brucei* and *Drosophila* SelD. Crustaceans GPxs from *L. vannamei*, *M. rosenbergii* and *S. serrata* are closely related to *L. vannamei* Trx1. Antioxidant *D. melanogaster* Trxr1 and Trxr2 are also related. Embryogenesis related Sel like BthD and SelK are grouped together. Putative antioxidant Sels like *L. vannamei* and *S. domuncula* SelM are closely related.

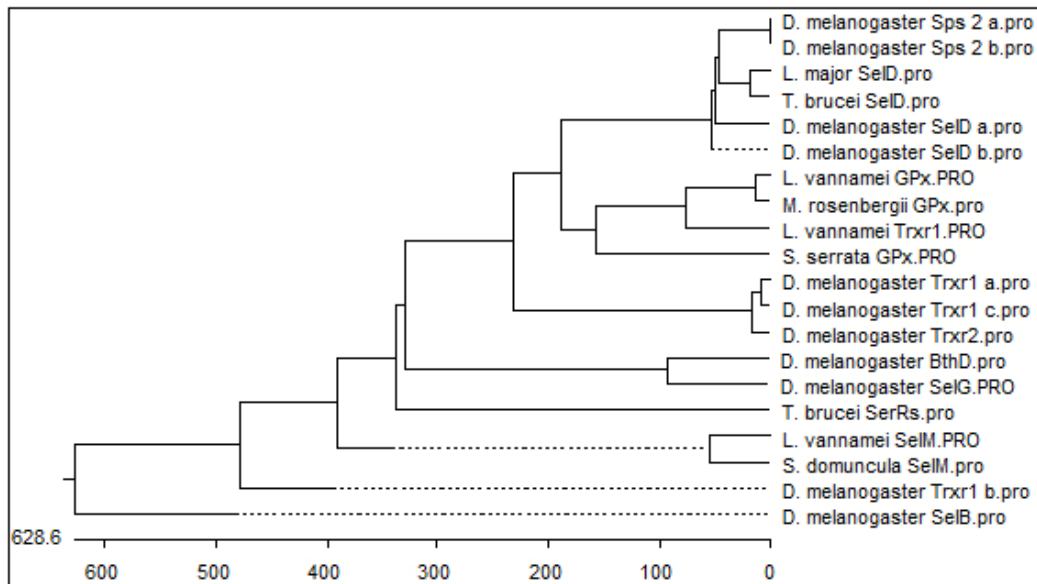


Fig. 1 Invertebrate Selenoproteins and two Trxr of *D. melanogaster* dendrogram elaborated with MegAlign 4.05 (DNASTAR Inc.). The length of each pair of branches represents the distance between sequence pairs, while the units at the bottom of the tree indicate the number of substitution events.

The information of the selenoproteome from *Drosophila* is the closer system studied to marine crustaceans. Since only few Sels appear to be encoded in the *Drosophila* genome (Martin-Romero et al. 2001), marine crustacean selenoproteome could be as relatively simple as that identified in *Drosophila*. Several Sels have been identified in invertebrates, but due to their importance in viability, development and physiology in experimental organisms as *Drosophila*, three of them are the most interesting to search for in the marine crustacean selenoproteome. The importance of SelD for cell function, cell proliferation and cell cycle progression in *Drosophila* has been demonstrated. It has also been shown that SelD is important for Sels synthesis and that its disruption results in impairment of Sels biosynthesis, ROS burst and lethality. Thus, it is very important to identify SelD in marine crustaceans to search for Sels biosynthesis pathways and possible control points in enzyme regulation. Sel BthD is expressed dynamically during *Drosophila* development and plays a general function in cellular metabolism and probably in protein secretion or processing. Elimination of BthD reduces animal viability. SelK discovery and study should be also an important study theme. Since this Sel is important in *Drosophila* viability it might be important in marine crustacean metabolism, it could also share the same physiological and developmental functions, but several studies should be done to test this prediction.

In summary, the identification and characterization of Sels in marine crustaceans is a recent field of research. Studies are still necessary to address questions about the combined effect of environment, physiological status and pathogen challenges to elucidate the role of the selenoproteome in marine crustaceans. That knowledge could be useful to propose strategies for the crustacean culture industry based on good health of the organisms and ultimately, good profits.

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