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Glucose and other hexoses transporters in marine invertebrates: A mini review

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Abstract Glucose and related hexoses are very important metabolic substrates. Their most important function is to provide quick fuel for most organisms in all three kingdoms because they are the first substrate for energy production in the form of ATP through glycolysis and the subsequent metabolic pathways. In this paper we review the current information about how glucose and related hexoses are transported across biological membranes to carry out their function either as a metabolic molecule or as energy store in marine invertebrate organisms. In these animals, there are two sugar transport systems that are mediated by the sodium/solute symporter family proteins (SGLT) and the major facilitative super-family proteins (GLUT). The most studied sugar transporters in marine invertebrates are involved with dietary sugar uptake, such as SGLT1, SGLT4, GLUT2 and GLUT5, however more studies need to be done to extend the knowledge about these and other sugar transporters involved in metabolic processes.

Keywords: facilitative, GLUT, SGLT, sodium-dependent, transport

Transporters of glucose and other hexoses

Glucose is the major product of carbon fixation by photosynthetic organisms and consequently, it is the most abundant molecule on earth. Glucose is found as a monomer or as a polymer, including cellulose, starch, glycogen and others. Hexoses importance resides in their variety of functions. They are structural components for all living cells, glucose is an important metabolic substrate, serves as a precursor for synthesis of many other molecules, and the most important function shared with related hexoses, is that it is the first fuel used by most organisms in all three kingdoms serving as quick substrate for energy production in the form of ATP through glycolysis and the subsequent metabolic pathways.

In higher organisms, glucose is mainly obtained directly from the diet when disaccharides and polysaccharides are hydrolyzed. After that, glucose needs to travel a long way to reach the target cells to be metabolized or stored. The first step is the transfer from the lumen of the small intestine to epithelium cells, followed by transport by blood circulation to each organ, tissue and cell. Due to the hydrophilic nature, these processes involve the transfer of glucose (and other hexoses) across the biological lipid bi-layer plasma cell membranes (Wilson-O'Brien et al. 2010).

This transport is mediated by integral transporter proteins which are classified based on phylogenetic and functional data (Wilson-O'Brien et al. 2010). Thus the hexose transporters belong to one of two protein super families: the sodium/solute symporter family (SSSF; (Reizer et al. 1994)) and the major facilitative super-family (MFS; (Marger and Saier Jr, 1993; Pao et al. 1998; Saier Jr, 2000)) whose Pfam numbers in the database http://pfam.janelia.org are PF00474 and CL0015 respectively.

Both sodium dependent and facilitated transport have been widely studied in humans and other mammals (Zhao and Keating, 2007; Aschenbach Jr et al. 2009). The Na^+-dependent glucose co-transporters form a family of proteins named SGLT which are coded by the genes SLC5A (Wright, 2001), whereas the Na^+-independent glucose transporters are clustered in the family of proteins named GLUT and the corresponding genes are known as SLC2A (Joost and Thorens, 2001). Little is known about sugar transport in invertebrate animals and even less in marine invertebrates; in this review we compiled the information to provide an overview and understand glucose and related hexoses uptake and importance.

Sodium dependent glucose transporter

The SGLT transports glucose or galactose with different affinities (Wright, 2001). The transport occurs via a secondary active transport mechanism because the Na^+-electrochemical gradient provided by the Na^+-K^+ ATPase pump is utilized to transport glucose into the cells against its concentration gradient (Wood and Trayhurn, 2003). The SGLT1 cDNA was first cloned from rabbit intestine by Hediger et al. (1987) and soon the human SGLT1 analogue was also found (Hediger et al. 1989); after that, the molecular era of intestinal glucose absorption studies arrived (Kellett, 2001). Currently, eleven SLC5A genes have been identified in the human genome and at least six proteins SGLT have been found to be inserted into the plasma membrane (Wright and Turk, 2004).

Some of these transporters are also found in invertebrate species including insects (Caccia et al. 2007); snails (Barber et al. 1985); shrimp (Blaya et al. 1998; Verri et al. 2001; Vilella et al. 2003), lobsters (Ahearn et al. 1985; Verri et al. 2001; Mandal et al. 2003; Sterling et al. 2009); horseshoe crab (Sterling and Ahearn, 2011), mussel (Louzao et al. 1993) and oyster (Hanquet et al. 2011). In particular, in the oysters a SGLT homolog has been sequenced (Huvet et al. 2004). The unavailability of nucleotide and protein specific sequences for most invertebrate marine species, led to the use of the alternative strategies that are mentioned below for the studies.

SGLT1 (SLC5A1). SGLT1 is largely responsible for glucose and galactose transport across the intestinal brush border (Stevens et al. 1984; Wright et al. 2011) and in the proximal tubules of the brush border membrane in kidney (Turner and Moran, 1982; Wright et al. 2011); therefore it was cloned from the small intestine of rabbit (Hediger et al. 1987). The deduced amino acid sequence is 664 residues long with a molecular weight of 73 kDa and shows no sequence homology to GLUT proteins. The protein secondary structure has 14 transmembrane helices (Figure 1) with both N-terminal and C-terminal located in the extracellular side of the membrane and containing a variable number of consensus sites for N-linked glycosylation (Turk et al. 1991). When the human SGLT1 sequence (GenBank accession no NP_000334.1) is submitted to BLAST analysis (Altschul et al. 1997) comparing to invertebrate SGLT proteins, such as that of the oyster *Crassostrea gigas* (GenBank accession no AY551098 (Huvet et al. 2004), they result 54% identical and 74% homologous. An hypothetical protein (GenBank accession no EFX74329) encoded by a gene found in the recently completed genome sequence (Colbourne et al. 2011) for the water flea *Daphnia pulex* is 50 and 55% identical to human and oyster SGLT1 proteins, respectively. The alignment of human, oyster and water flea proteins is shown identifying the fourteen transmembranes domains in Figure 1.

SGLT1 is present in the crustacean hepatopancreas brush-border membrane cells where the Na^+/D-glucose co-transport occurs via an electrogenic Na^+-dependent, carrier-mediated, high-affinity mechanisms, while in basolateral membrane cells, the glucose transporter is not Na^+-dependent (Blaya et al. 1998; Verri et al. 2001; Vilella et al. 2003). Besides, Vilella et al. (2003) showed that in the presence of an interior negative membrane potential, the Na^+/D-glucose co-transport is strongly activated by H^+.

Evidence for the presence of SGLT was obtained using phloridzin, a specific inhibitor of Na^+-dependent glucose transporter (Hopfer et al. 1973; Verri et al. 2001; Vilella et al. 2003). Recently, studies involving both, physiology and molecular biology have been done in the hepatopancreas brush-border cells from lobster *Homarus americanus* (Sterling et al. 2009) and from the horseshoe crab *Limulus polyphemus* (Sterling and Ahearn, 2011). These authors measured D-[$^+$H]-glucose uptake with and without Na^+. Moreover they used a rabbit anti-SGLT1 synthetic peptide in immunoblotting assays and found cross-reaction with a protein of similar molecular weight of the mammalian SGLT1 (75 KDa) in brush-border cells and total hepatopancreas.

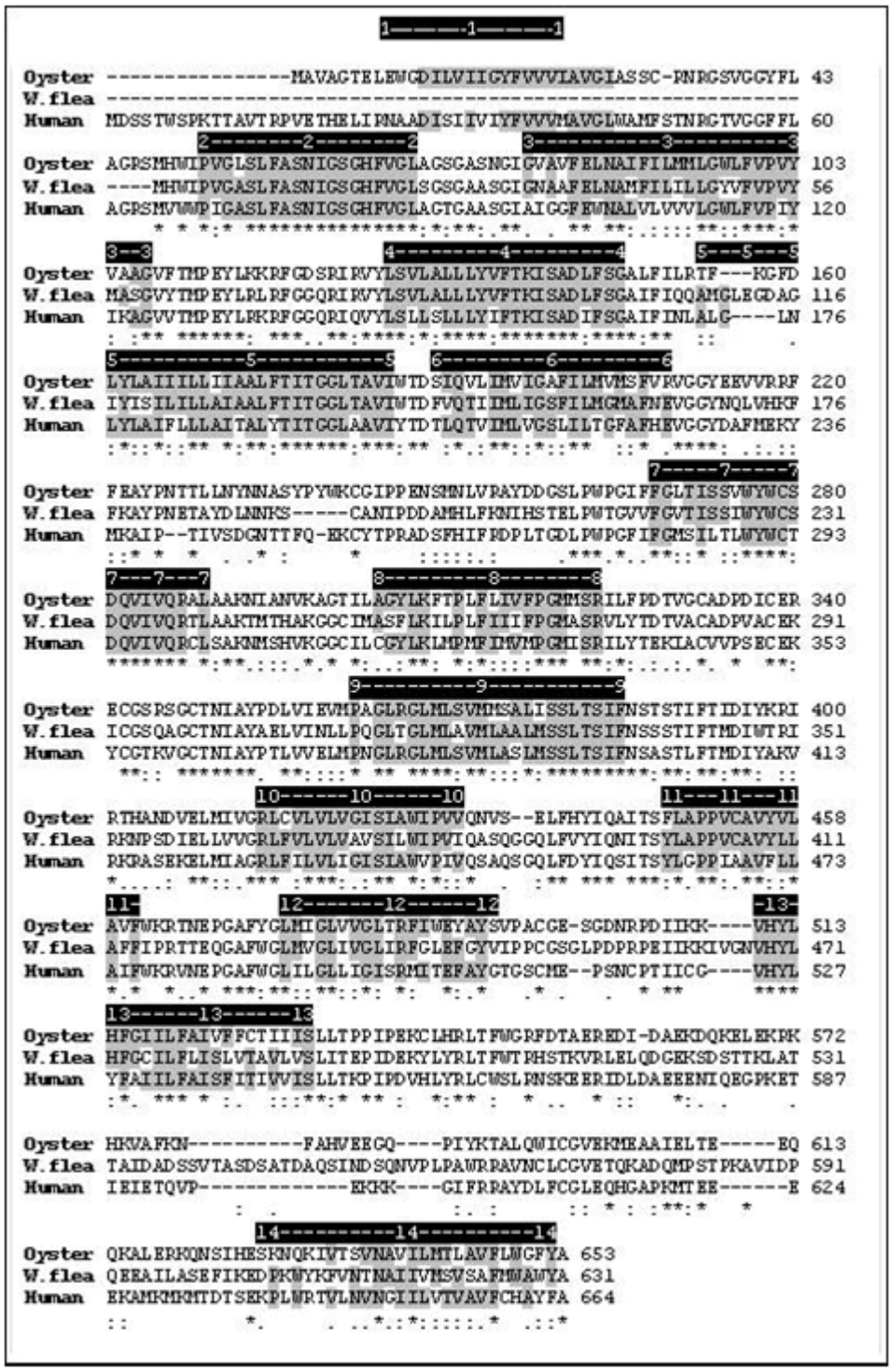

Fig. 1 Sequence alignment of the deduce amino acid sequence of human SGLT1 (GenBank accession no NP_000334.1), oyster SGLT1 (GenBank accession no AY551098) and water flea hypothetical protein (GenBank accession no EFX74329). The alignment was performed with the CLUSTAL W algorithm with open gap cost = 10 and gap extension cost = 0.2. Positions exhibiting absolute identity are indicated with *; those with conserved substitution with a dot. The position of the fourteen transmembrane segments predicted for human SGLT1 by PHDhtm (Combet et al. 2000) is shown with the number dashed line at the top of the sequence alignment and with light gray identical amino acids between them.

In addition, these studies report a mRNA sequence from *L. polyphemus* (Meusemann et al. 2010) that when analyzed by BLAST, has a 54% identity that raises to 78% considering conservative replacements to the mouse SGLT1 protein (Tabatabai et al. 2001) and similarly, 57% identity and 78% with positive replacements to the rat SGLT1 (Stearns et al. 2010). Meanwhile, analysis by BLAST of translated EST (expressed sequence tags), sequence EX471402 from *H. americanus* (Towle and Smith, 2006) was found to have 74 and 75% amino acid identity to the rabbit and mouse SGLT1s, respectively. Also, the translated product of EST FD483413 has 58 and 77% identity and positive replacement, respectively, to the oyster SGLT1.

Evidence for the presence in mollusc of SGLT came from the detection in the oyster *C. gigas* of inhibition of D-glucose uptake by phloridzin in different oyster vesicular cells tissue and also, the detection of higher expression of SGLT in gills and mantle edge, as measured by RT-qPCR (Hanquet et al. 2011).

As mentioned above, SGLT is present in hepatopancreas cells, however hepatopancreas is an organ that is composed by five different cell types: E, F, R, B and M cells (Verri et al. 2001), therefore follow up studies were aimed to determine the type of glucose transport present in each type of cell. Vilella et al. (2003) measured D-glucose uptake into the R and B cells in the presence and absence of phloridzin, finding that phloridzin inhibited the Na^+/D-glucose co-transport in the B, but not in the R cells of the kuruma prawn *Marsupenaeus japonicus*, although glucose was transported in both B and R cells, which suggests that in R cells, a Na^+-independent D-glucose transport is present. In another study on hepatopancreas cells of the lobster *H. americanus* (Sterling et al. 2009) using a polyclonal rabbit anti-mouse SGLT1 antibody, the authors found a strong cross reaction with SGLT1-like in F cells and a weaker one in R and B cells, but not with E cells. As seen before, hepatopancreas is a very important organ in crustaceans for dietary glucose absorption, however it is also known that the intestine plays in addition an important role in this mechanism (Ahearn et al. 1985; Verri et al. 2001). A very interesting study developed in non-vertebrate organisms was done in *Aphidius ervi* (Caccia et al. 2007) where the presence of SGLT1-like in the apical membrane of the midgut epithelium cells was shown by physiologic and immunocytochemical approaches, thus this model is similar to the previously described for mammals. See Kellett (2001) for a review.

Since the intestine is an organ that absorbs nutrients that are not taken up by the hepatopancreas, recently, Obi et al. (2011) investigated the type of glucose transporters that are present in the intestinal epithelium cells from the lobster *H. americanus*. First, they found that at pH 7.0, labelled D-[^{3}H] glucose transport from the lumen presented a hyperbolic function when the concentration of glucose incremented. After that, they showed that the D-[^{3}H] glucose transport was significantly inhibited in the presence of phloridzin, indicating the presence of SGLT1 in the mucosal membrane of the lobster intestine, as reported for mammals (Drozdowski and Thomson, 2006) and insects (Caccia et al. 2005; Caccia et al. 2007; Bifano et al. 2010).

A few studies have reported kinetic constants for Na^+-dependent glucose uptake in marine invertebrates. When lobster hepatopancreatic poly(A^+)RNA induced Na^+-dependent glucose uptake in *Xenopus laevis* oocytes in D-glucose saturation conditions, an apparent K_m of 0.47 ± 0.04 mM was calculated (Mandal et al. 2003). The apparent K_m for glucose uptake in labial palps vesicular cells from the oyster was 0.717 mM (Hanquet et al. 2011). Furthermore, the K_m for glucose uptake in lobster intestine is lower (15.2 µM) than in hepatopancreas (Obi et al. 2011). This can be explained because the hepatopancreas is localized before the intestine in the gastrointestinal tract, therefore, the dietary glucose concentration is higher in the hepatopancreas ducts, thus the transporter proteins respond at this higher concentration, however by the time dietary glucose reach the intestine, the concentration had been significantly reduced and a high affinity transporter proteins are required.

SGLT4 (SLC5A9). Until 2004, the specific functions of SGLT4 was not known, solely that it is widely expressed in the body (Wright and Turk, 2004), but in 2005 Tazawa et al. (2005), reported a cDNA clone for SLC5A9/SGLT4 isolated from human small intestine that was functionally characterized. SGLT4 is expressed in small intestine and kidney and one of its physiological functions is Na^+-dependent fructose transport (Gerich, 2010). There is evidence that SGLT4 is present in hepatopancreas membrane cells of the lobster *H. americanus* (Sterling et al. 2009) and the horseshoe crab *L. polyphemus* (Sterling and Ahearn, 2011). In both, the lobster and the horseshoe crab, fructose uptake was measured in hepatopancreas brush-border membrane vesicles (BBMV) and basolateral membrane vesicles (BLMV), finding a lower fructose transport in absence of sodium, while in presence of sodium, the uptake of this sugar was not affected by high glucose concentration. These results

indicate that in both brush-border and basolateral membranes of these animals, fructose uptake is sodium dependent and the transporters are different to those for glucose. Besides, using a rabbit anti-human SGLT4 antibody, Western blot analysis indicated the presence of an orthologous protein consistent with the SGLT4 from mammals.

Previous studies have shown that the D-fructose transport mechanisms in crustacean hepatopancreas cells appear to be similar to the mammalian intestine and kidney counterparts (Gould and Holman, 1993; Drozdowski and Thomson, 2006), and later described in wasps (Caccia et al. 2007), where D-fructose transport is facilitated by GLUT2-like in basolateral membranes and by GLUT2-like and GLUT5-like in brush border membranes. However in both *H*. *americanus* and *L*. *polyphemus,* D-fructose absorption appears to depart from this transport paradigm because SGLT4-like is present at both, brush-border and basolateral membranes and GLUT2-like and GLUT5-like are localized at the basolateral membranes rather than at brush-border membranes. Additional information about SGLT4-like in marine invertebrates are the kinetic constants in the presence of extracellular sodium for fructose influx in hepatopancreas E cells from *H*. *americanus*, with a K_m of 3.25 mmol l^{-1} and a J_{max} of 548.53 nmol mg^{-1} protein min^{-1} (Sterling et al. 2009).

Facilitative glucose transporters

GLUT family proteins act as facilitative glucose and other hexoses transporters since they utilize the diffusion gradient of sugars across plasma membranes. The first transporter to be isolated was cloned from a HepG2 cell line (Mueckler et al. 1985). After that, studies of identification of four new GLUT family members were conducted (Wood and Trayhurn, 2003). Finally with the completion of The Human Genome Sequencing Project new members were described. Currently, 13 members (Joost and Thorens, 2001) plus a duplication of GLUT3 named GLUT14 (Wu and Freeze, 2002; Augustin, 2010; Thorens and Mueckler, 2010) are known. All GLUT protein members have been named by consensus GLUT1-14 (genes SLC2A1-14) and GLUT13 is named HMIT (H^+ -coupled myo-inositol transporter) (Joost et al. 2002).

GLUT transporters are expressed in every cell of the body with specific physiological role in the tissue to contribute in the control of glucose homeostasis. All of them have features in common such as the predicted 12 transmembrane spanning domains, with both amino- and carboxyl-termini located intracellularlly and harbour a unique N-linked glycosylation site (Mueckler et al. 1985), moreover these transporter are highly conserved in most species (Höglund et al. 2011) and the three-dimensional structure has been predicted (Salas-Burgos et al. 2004). Little is published about GLUT proteins in marine invertebrate organisms. Although there is a report for a GLUT1 in the shrimp (Somboonwiwat et al. 2006), the authors do not present solid evidence for its function. However since GLUT2 and GLUT5 have been studied in different species, we describe them separately.

GLUT2 (SLC2A2). GLUT2 cDNA was cloned from human liver cDNA libraries and the deduced protein is 524 amino acids. This protein has been widely studied in humans, where is found in different tissues such as liver, pancreas islets, kidney, small intestine and brain (Fukumoto et al. 1988; Ohtsubo et al. 2005; Marty et al. 2007). Noteworthy, GLUT2 is able to transport not only glucose, but also other hexoses with specific affinity.

GLUT2 is a low affinity transporter for glucose with a K_m of ~17 mM (Johnson et al. 1990) and a K_m of ~92 mM, ~125 mM and ~76 mM for galactose, mannose and fructose respectively (Colville et al. 1993). Moreover, in the case of glucosamine, GLUT2 transports it with high affinity (Uldry et al. 2002). The capacity of GLUT2 to transport fructose is due to the absence of the QLS motif in helix seven present in all the GLUT proteins than do not bind fructose (Seatter et al. 1998).

Although this review aims to lay out sugar transporter in marine invertebrates, in this particular case, we consider necessary to mention GLUT2 from other species, since the role of this protein in dietary sugar uptake has been a little controversial. A classical model of mammal intestinal sugar transport proposed the presence of GLUT2 in basolateral membrane of intestinal cells but not in the brush border membrane (Wright, 1998). However later studies showed evidence of the presence of GLUT2 in both, basolateral and brush border membranes when glucose or fructose concentration in the luminal side is high, implying the GLUT2 recruitment to the brush border membranes (Helliwell et al. 2000; Kellett and Helliwell, 2000; Kellett, 2001; Au et al. 2002; Cheeseman, 2002; Kellett and Brot-Laroche, 2005).

Interesting studies have been also done in invertebrate organisms. Caccia et al. (2005) using immunodetection techniques, found that a GLUT2-like transporter is present in the apical membrane of midgut cells from the insect *A. ervi* larvae, and later these authors found in the same animal, using glucosamine and galactose, that the transport of glucose in the apical membranes was almost entirely suppressed, suggesting the presence of GLUT2 and SGLT1, however they mention that GLUT2 intensity sometimes was variable or even absent, therefore they speculated that as the well described model for mammalian intestine, GLUT2 in *A. ervi* is recruited from intracellular vesicles to the cell membrane (Caccia et al. 2007).

To characterize D-glucose and D-fructose transport across marine invertebrate animals gastrointestinal tracts, some studies have been carried out. In the lobster *H. americanus* intestine, GLUT2 was localized in both basolateral and apical membranes, but the results were not overwhelming since in the presence of luminal phloretin (a GLUT2 inhibitor), fructose transport was significantly decreased which indicated luminal GLUT2 presence, however, phloretin was not able to affect luminal glucose transporter, suggesting that brush border glucose transporter in lobster intestine is mainly mediated by SGLT1 (Obi et al. 2011).

So far, it is clear that GLUT2 transports either glucose or fructose at both basolateral and apical membrane in the intestine of mammals, insects and crustaceans. In the lobster *H. americanus* hepatopancreas cell membranes, some differences have been reported to the mammalian paradigm, since using a rabbit anti-rat GLUT2 antibody in Western blot assays, there was cross reaction in all kind of hepatopancratic cells (E, R, F, B), but the cross reaction was localized at the basolateral membranes only, and SGLT4 (sodium dependent co-transporter) was in charge of fructose transport at both cell poles (Sterling et al. 2009). The research done in other marine invertebrate organism confirmed the differences between the well established mammalian model and the mechanism utilized by some of them. The chelicerate horseshoe crab *L. polyphemus* was shown to have GLUT2 transporter restricted to the basolateral membrane in hepatopancreas cells and SGLT4 is present at both, basolateral and apical cell poles (Sterling and Ahearn, 2011).

GLUT5 (SLC2A5). GLUT5 transporter belongs to the class II of glucose transporter family. All the members of the class II have a specific feature, that is their ability to transport fructose rather than glucose which has been linked to the presence of the NXV/NXI motif in helix seven (Manolescu et al. 2007). The first GLUT5 characterized was cloned from human small intestine (GenBank accession no M55531), later GLUT5 was isolated and cloned from mouse small intestine also (GenBank accession no NM_019741) (Kayano et al. 1990; Corpe et al. 2002). In both species the deduced protein is composed of 501 amino acids residues, with 83% of identity. GLUT5 is expressed in mammalian small intestine, kidney (Corpe et al. 2002; Jones et al. 2011) and testis (Burant et al. 1992; Angulo et al. 1998). In these tissues GLUT5 transports fructose with a K_m of ~6 mM and is not inhibited by cytochalasin B, phloretin or phloridzin (Burant et al. 1992; Mate et al. 2001).

As in vertebrate animals, GLUT5 transporter has been found in gastrointestinal tract tissues such as intestine and hepatopancreas of invertebrates organisms. Unfortunately in these last ones there are no complete sequences to allow more molecular studies as in mammals; however there are a few very interesting studies about GLUT5. Clear localization of GLUT5 protein transporter in the lobster *H. americanus* intestine cells, came by using a goat anti-rabbit FITC labelled GLUT5 polyclonal antibody for immunohistochemical analysis (Obi et al. 2011). A strong FITC signal from the luminal border of the intestine cells was found, while no signal was observed at the basolateral side, indicating that GLUT5 in the lobster intestine transports fructose from the luminal side as occurs in mammals and insects (Drozdowski and Thomson, 2006; Caccia et al. 2007; Douard and Ferraris, 2008). Contrary to most findings, Western blot assays showed that in hepatopancreas cells of the crustacean *H. americanus* and the chelicerate *L. polyphemus*, GLUT5 was not present in the apical membrane, moreover it is localized in the basolateral side and specifically in the lobster is restricted to F and B hepatopancreas cells (Sterling et al. 2009; Sterling and Ahearn, 2011).

Information from non-hexoses transport focused research

The current knowledge about dietary sugar transport in invertebrate marine animals indicated that the transport is mediated by two systems (SGLT and GLUT) depending of hexoses concentration, either from mucosal to serosal or serosal to mucosal direction. Two different models representing sugar absorption in these organisms can be proposed (Figure 2a-b).

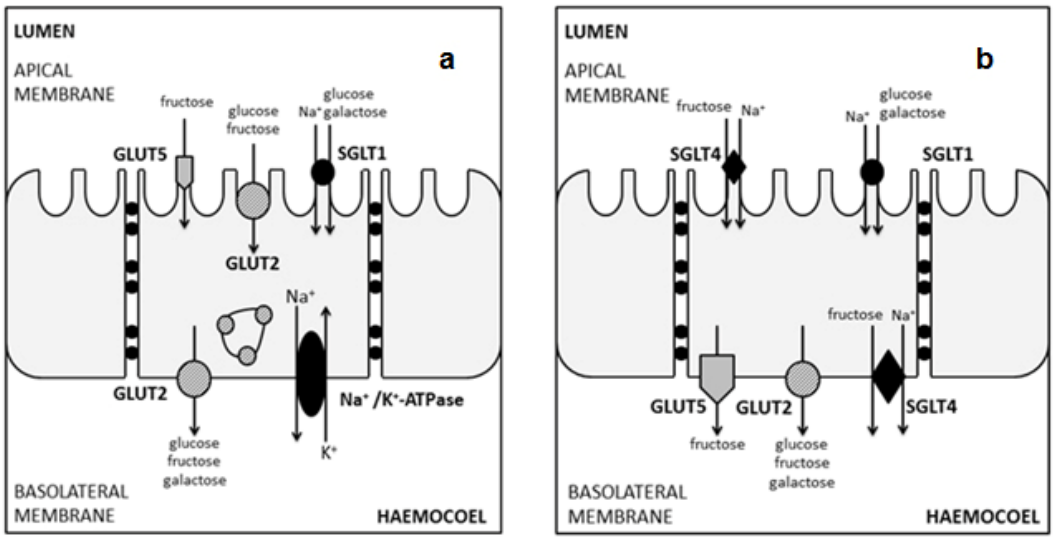

Fig. 2 Two models for sugar absorption in invertebrate marine animals. (a) Hexoses transporter in epithelial cells of intestine of some marine invertebrate organisms. At the apical pole of the cell are present both, Na^+/glucose or galactose co-transport by SGLT1 and facilitated fructose (GLUT5, GLUT2) or glucose (GLUT2) transport, GLUT2 is probably recruited from cytoplasmic stored to the brush border membrane. At the basolateral pole, the Na^+/K^+ pump ATP dependent restore the electrochemical gradient, and the hexose uptake is facilitated by GLUT5 (fructose) and GLUT2 (glucose, galactose or fructose) only. (b) Hexoses transporter in epithelial cells of hepatopancreas of some marine invertebrate organisms. Glucose or galactose and fructose transport sodium dependent is done by SGLT1 and SGLT4 respectively in the apical side of cell. At the basolateral side SGLT4 sodium dependent transport fructose and the facilitative transporters GLUT2 and GLUT5 transport glucose or galactose and fructose respectively.

Other studies done in marine invertebrate organisms not focusing in sugar transporters have provided interesting findings. The glucose transporter protein more widely studied in mammals is the facilitative GLUT1 (Carruthers et al. 2009) which has been also cloned from some terrestrial invertebrates cDNAs (Escher and Rasmuson-Lestander, 1999), yet little information is available for marine invertebrates. An ESTs (GenBank accession no. BQ563164) from *Artemia franciscana* related to *Drosophila melanogaster* DmGLUT (GenBank accession no. AF064703) was reported (Chen et al. 2003). Besides, Somboonwiwat et al. (2006) studied changes in gene expression by differential display PCR in haemocytes of the shrimp *Penaeus monodon* after infection with the bacteria *Vibrio harveyi* and found between the genes up-regulated a glucose transporter 1 (GLUT1 for protein) with a 59% homology to that of *Drosophila melanogaster* even though no sequence information was deposited in the GenBank data.

The author mentioned that glut1 reached its highest level early after infection, indicating that hemocites required more energy for cellular immune processes than in the normal state. An interesting article focused on the mechanism for virus infection in the white shrimp *Litopenaeus vannamei* showed that the white spot syndrome virus (WSSV) entry *via* occurs by the interaction between WSSV envelope proteins and a transmembranal protein of this shrimp. This transmembrane protein is a major facilitator superfamily member and has been named GLUT1, the cDNA was fully sequenced (GenBank accession no HQ620544) and the deduced primary structure sequence consists of 569 residues. The structural analysis of the deduced protein revealed all the characteristics of a facilitator transporter protein (Huang et al. 2012), however when a comparison of this protein with the human GLUT1 (GenBank accession no NP_006507.1) and with the water flea hypothetical GLUT1 (GenBank accession no GL732623.1) is done using BLAST, very low homology is found, suggesting that is not an homolog of the classical vertebrate GLUT1.

On the other hand, to gain insight into osmoregulatory and other compensatory mechanisms that accompany acclimation to salinity reduction in the green crab *Carcinus maenas*, changes in transcript abundance in gills tissue was analyzed applying DNA microarrays. Many genes were up regulated

including transport proteins and specifically a sodium/glucose co transporter, although probably in this particular case, and because of the type of treatments, might be the Na^+ transporter (Towle et al. 2011). Likewise in the shrimp *Litopenaeus setiferus,* glucose uptake in hepatopancreas brush border vesicles is stimulated in the presence of inwardly directed gradients of either sodium or potassium (Simmons et al. 2012), and these authors suggest that SGLT1-like in this shrimp exhibit a broader action specificity than the specificity of most animals described previously.

CONCLUDING REMARKS

Since sugar is very important for most living organisms and knowing that they cannot diffuse across the cell membranes, it is evident that sugar transporter proteins must be present to carry these molecules either in favour or against the concentration gradient. Due to the characteristics of the organs, tissues, cells, membranes and sugar molecules *per se*, multiples hexose transporter exist. Many studies have provided evidence for the presence of these transporters in marine invertebrate organisms, especially those involved with dietary sugars uptake from the digestive tract to circulatory system, however, is important to obtain information about the genes, cDNAs and proteins sequences necessary for a better understanding of the sugar transport mechanisms. On the other hand, the big picture of the sugar transporters refers not only to their functions in dietary sugars uptake, but also the delivery from the circulatory system to all tissues and the timely release from the cellular stores in some tissues, to be delivered to other cells or tissues. Now that more and more genome sequences are being completed, the information gathered from those studies is a milestone to expanding the scope and understanding of the hexoses transporter mechanisms and their milieu in relation not only to diet, but also to particular responses to internal, as well as external changes that affect the animals. Invertebrate animals share with terrestrial invertebrates many of the basic biochemical and physiological central responses, but, as they live in a completely different environment, they may have developed specific strategies to deal with particular conditions. For example, it is known that some crustaceans can endure extreme hypoxia conditions relying on anaerobic glycolysis and glucose mobilization, probably glucose transporters are key players in these processes. Future studies aimed to understand responses to bacteria and virus infections may reveal their importance also in otherwise apparently distant processes.

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