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Review Article

Ion Transporters in Shrimps

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Abstract

Ion transporters are integral proteins in the membrane that regulate cellular absorption and excretion of inorganic ions. Ion transport through cell membranes and organelles is necessary for performing osmoregulatory functions in any organism. The function and mechanisms of various ion transporters are well established in higher vertebrates. However, shrimps, being invertebrates, many of the ion transport mechanisms differs from the fish. This mini review has been aimed at discussing the ion transporters in shrimps and their possible mechanisms.

Keywords: Ion transporters; Nutrient transporters; Shrimps

Introduction

Ion transport is the movement of salts and electrolytes in the form of ions within living systems. It can occur through diffusion or through active transport. It is extremely important for all species in their essential activities. Transporters participate in homeostasis of calcium, transportation of nutrients (glucose, proteins) and ions (K^+, Na^+, and $Ca2^+$), extracellular pH regulation, excretion of ammonia, osmoregulation and signal transduction (activation of protein synthesis, cell division etc) besides maintaining the cell integrity.

The crucial component for transporting ions actively in shrimp is Sodium-potassium ATPase (Na^+/K^+ ATPase) pump which acts as a driving force for other transporters like (Sodium Potassium Chloride co-transporter (NKCC), glucose transporters, amino acid transporters etc. Calcium transporters (plasma membrane calcium ATPase, PMCA and $Na^+/Ca2^+$ exchanger, NCX) transport calcium to the blood during post molt. Calcium channels (sarcoendoplasmic reticulum calcium transport ATPase, SERCA and inositol 1,4,5-triphosphate receptor, IP3R) discharge calcium depot from sarcoplasmic reticulum to the cytoplasm periodically. Another transporter, ruthenium red uniporter is used for the uptake of calcium in mitochondria. Failure of any of the transporters will have negative impact on shrimp physiology. Furthermore, the understanding of these transporters will be helpful to know about the nutritional physiology that in turn leads to develop the efficient feed.

Sodium-potassium ATPase

Structure: Na^+/K^+ ATPase are a plasma membrane transport protein of the gills and excretory organs of shrimps. The structure of Na^+/K^+ ATPase of shrimp is similar to that of teleost. It is composed of two subunits (Figure 1) [1], α subunit (95-101 KDa) and β subunit (38-40 KDa). α subunit is catalytic; ions, magnesium, ATP and ouabain binds at this component. However, the activity of Na^+/K^+ ATPase is supposed to be governed by β subunit.

Seawater shrimps: Na^+/K^+ ATPase are the primary ion pump and crucial component in osmotic and ionic regulation. It helps in the excretion of NaCl. With the help of ATP and magnesium as a cofactor, three sodium ions (Na^+) leaves the cell replacing 2 potassium ions (K^+). Therefore, the pump maintains intracellular high K^+ and low Na^+. Na^+ gradient created by the pump acts as a driving force for NKCC that is responsible for transportation of ions from hemolymph to gills. Besides sodium and potassium, chloride ions are also transported into the cell (Figure 2) [2]. The electronegativity of the cell increases due to accumulation of chloride which moves to the less negatively charged seawater via chloride channel passively. Na^+ follows the gradient and moves from blood (positively charged) to seawater (negatively charged) while the K^+ moves out of the cell via K^+ channel and is recycled by Na^+/K^+ ATPase.

Freshwater shrimps: In freshwater shrimps, sodium potassium ATPase helps in cell volume regulation. It maintains the right concentrations of ions and helps in absorption of sodium chloride (NaCl). The transport mechanism has been shown in Figure 3 [2]. Failure of the pump causes cell to swell and lysis. Furthermore, when the cell begins to swell due to osmosis, Na^+/K^+ ATPase pump gets activated automatically as it changes the internal concentrations of Na^+ and K^+ to which the pump is sensitive. Na^+ is absorbed in the presence of ATP through ENaC (Na^+ channel) driven by H^+ extrusion by means of V (H^+) - ATPase activity present in the gills [3]. Na^+ is then delivered to hemolymph by Na^+/ K^+ ATPase in exchange for K^+. Apical flange Cl-/ HCO3- exchangers are responsible for the transportation of Cl- [4] to the pillar cell flanges while Cl- moves out to the septal cells or directly into the hemolymph via basal Cl- channels.

Na^+/K^+ - ATPase in ammonia ($NH4^+$) excretion: Na^+/K^+ ATPase pump reveals a new binding site when the level of $NH4^+$ is high to which $NH4^+$ binds. Under these circumstances, Na^+/K^+-ATPase activity doesn't depend on K^+ ions. K^+ in *Callinectes sapidus* has been replaced by $NH4^+$ which is responsible for the activation of Na^+/K^+-ATPase pump [5]. Similar mechanism has been found in freshwater shrimp (*Macrobrachium olfersii*) for the removal of ammonia [6].

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Calcium activated chloride channel (Cacc): Cacc is another critical component in osmotic regulation. It is located in gut, antennal glands and gills epithelial cells. It regulates calcium concentration. Calcium transport across epithelium takes place at the apical side passively while along the basolateral side occurs both passively and actively during intermolt (Figure 4) [7]. Transporters involved in calcium transport are ATP-dependent PMCA, NCX, SERCA and IP3R. Na^+ gradient generated by Na^+/K^+- ATPase pump drives both PMCA and NCX. These transporters provide efflux mechanisms to transfer cytosolic calcium into the blood. Calcium transport during the intermolt stage is less as compared to post molt as stored calcium is discharged during post molt. Endoplasmic Reticulum (ER) serves as a depot of calcium during molting. ER membrane possesses SERCA and IP3R calcium channels. SERCA transports calcium in the presence of ATP from the cytoplasm to the organelle interior

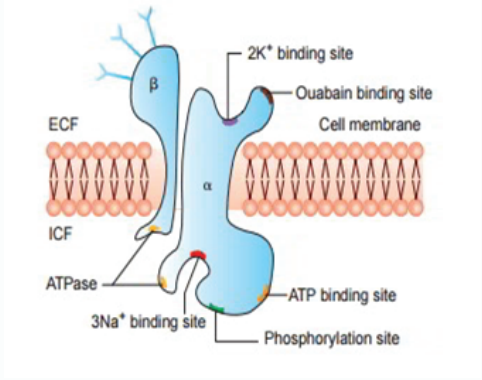

Figure 1: Structure of Na^+K^+-ATPase.

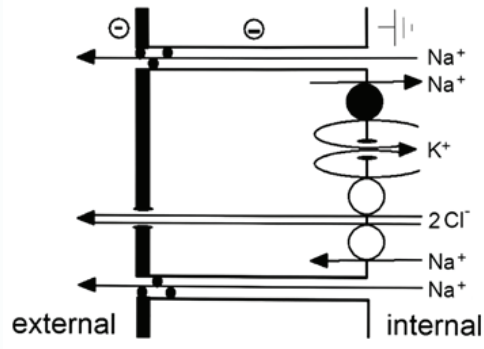

Figure 2: Nacl transport mechanism seawater shrimps.

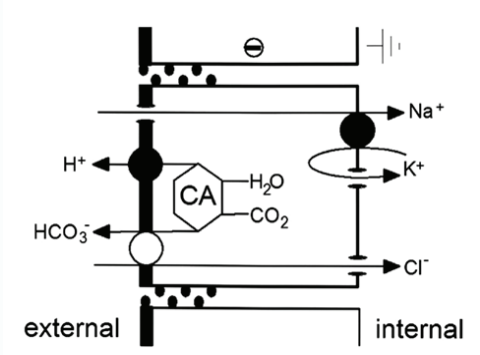

Figure 3: Nacl transport mechanism freshwater shrimps.

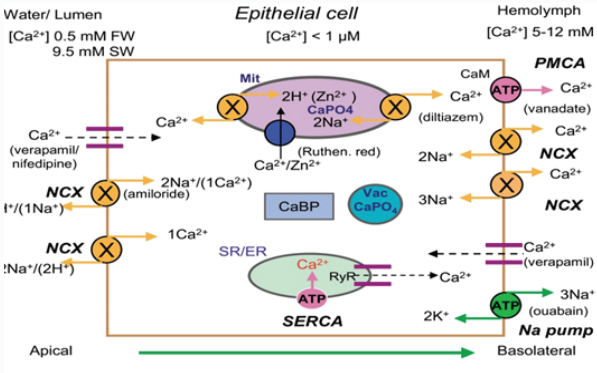

Figure 4: Ca2+ transport mechanism. Inhibitors have been given in parentheses. Sarcoplasmic Reticulum (SR); Endoplasmic Reticulum (ER); Calcium-binding Protein (CaBP); Calmodulin (CaM); Mitochondria (Mit); Vacuole (Vac); Freshwater (FW); Seawater (SW); and Ryanodine Receptor (RyR).

while IP3R discharges calcium depot from the SR to the cytoplasm periodically. Calcium released forms will be taken up by mitochondria via ruthenium red uniporter. Zinc (Zn) and Copper (Cu) inhibits calcium transport.

Nutrient Transporters

Aminoacid transporter: The amino acid transporter depends on Na^+ or K^+ for the uptake of amino acid and the activity increases by acidic pH. Potassium-coupled amino acid transporter (KAAT1) makes use of potassium gradient and membrane potential for the transportation of various neutral amino acids. In absence of sodium or potassium, metallic ions (Cu, Co, Zn, Cd, or Mn) stimulate transport of the amino acids. Amino acids make complexes with metals on peptide transporter and are transported as a bis-complex consisting of two amino acids and a metallic cation like Leu-Zn- Leu through the corresponding cellular membrane. Metal mimics peptide bond in dipeptides and therefore the transporter accepts the complex as such. PEPT1, PEPT2, PHT1 and PHT2 are the possible carrier systems supporting amino acid transfer. Moreover, glycine (amino acid) requires Na^+ ions and ATP for its transport. In general, the amino acid transporters use the transapical sodium (or potassium) gradient and basolateral transmembrane potential created by Na^+/K^+ ATPase pump, to move the amino acids into the cell by symport with sodium (or potassium) as it flows down its concentration gradient into the cytoplasm (Figure 5). Besides this, another transporter called B-system transports sodium-dependent L-leucine and other neutral amino acids.

Glucose transporter: Na^+- dependent co-transport is responsible for glucose transport in crustaceans [8] including freshwater shrimps [9] and seawater shrimps [10]. Moreover, shrimps are the only invertebrates that dependent either on Na^+ or K^+ for sugar uptake. Unlike B cells of hepatopancreas where glucose transport is Na^+ dependent, R cells exhibits Na^+ independent sugar transport.

D-glucose is absorbed by shrimp hepatopancreas by a Na^+/K^+ co-transporter. This transporter differs from vertebrates Na^+-dependent D-glucose (SGLT1) uptake process and is similar to the mammals K^+-dependent SGLT4 transporter. Na^+ gradient is created by Na^+/K^+ ATPase pump and as Na^+ flows back through the membrane via co-transporter, it moves glucose into the cell against its electrochemical gradient (Figure 6) [11].

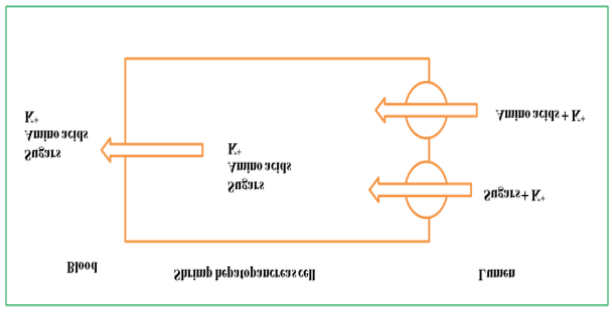

Figure 5: Potassium dependent nutrient transport.

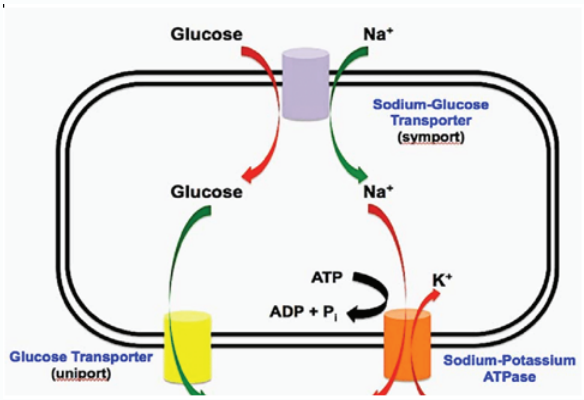

Figure 6: Sodium dependent Glucose transport.

The use of both K^+ and Na^+ by sugar and amino acid transporters in shrimp digestive tract allows these animals to use K^+ as a driver cation for nutrient uptake when they are largely herbivorous (larvae) and change co-transporters to Na^+ later in life when they become carnivorous. This information, plus the findings that metallic cations stimulate essential amino acid uptake when the absorption environment is acidic, provides information for the potential development of two growth promoting artificial diets for shrimp in aquacultural facilities, one used during early development and one employed later in life. It is suggested that the combination of two such diets, based on an understanding of shrimp nutritional physiology, might provide faster growth than present diets and could therefore reduce the time to market and the cost for the farmer by itself. These features are identical with those possessed by the mammalian SLC5A9/SGLT4transporter, indicating that an invertebrate analog of this protein can exist in shrimps.

Conclusion

Ion transporters are transmembrane proteins necessary for maintaining the shrimp physiology thriving in freshwater as well as saline environments. Na^+/K^+ ATPase pump; calcium transporters (like PMCA, NCX, SERCA, and IP3R); glucose transporters (sodium and potassium dependent) and amino acid transporters (like KAAT1) are responsible for the transport of ions and nutrients across the plasma membrane of the cell. As feed are the main and the costly component in the aquaculture. Understanding the cellular transport mechanisms will help in enhancing the growth by determining the effective components of shrimp diet. A few studies have been conducted in shrimps; however the presence of transporter like PEPT is yet to be known in shrimps. Further research is necessary to be carried out to better know about the complete physiology of shrimps.

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