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ROLE OF GILL CHLORIDE CELL IN TELEOST GROWTH

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INTRODUCTION

Teleost fish inhabit diverse aquatic environment and face osmoregulatory problems. Osmoregulation is the result of integrated ion and water transport activities of the gill, kidney and intestine, creating ionic and osmotic gradients between the body fluid and external environment. Gills are the most important extrarenal organ responsible for ion regulation (Perry, 1997; McCormick, 2001). Freshwater teleosts face water load and salt loss through their permeable body surfaces, most of which are occupied by the gill epithelia. To overcome these problems, they discharge excess water by producing dilute urine in the kidney and take up ions through the gill epithelia. However, marine teleosts face with water loss and salt load, and the water loss is compensated by drinking seawater and by absorbing water across the intestine, while excess ions are excreted from the gill and kidney (McCormick, 1990, 1995; Fiol and Kultz, 2007).

Stenohaline teleosts such as zebrafish can tolerate a narrow range of salinities; however, euryhaline species such as tilapia, salmon and eels can tolerate a very wide range of salinities (Ayson et al., 1994; Bindons et al., 1994; Ando et al., 2003). These euryhalinity or stenohalinity of teleosts primarily determined by their ability of functional alteration and plasticity of gill chloride cells, also known as mitochondrion-rich cells or ionocytes (Maina, 1991; Ayson et al., 1994; Ando et al., 2003). Chloride cells, the principal ion transporting cells in the gill epithelium was first identified by Keys and Wilmer (1932), while describing mitochondria-rich cells responsible for the secretion of Cl- in seawater adapted teleosts. These cells are characteristic of marine fishes in which an extrarenal mechanism for the elimination of excess of salts from the body fluid is necessary for correct osmoregulation and maintaining homeostasis (Datta Munshi, 1964; Chang et al., 2001). In addition, chloride cells are also involved in acid-base regulation and play an important role in adaptation to various osmotic and ionic aquatic environments (Pisam and Rambourg, 1991; Kaneko et al., 1995, 2002).

The choride cell contains numerous mitochondria and exhibits a greatly amplified basolateral cell surface richly endowed with Na+,K+-ATPase. Na+,K+-ATPase activity is a membrane-bound enzyme in teleost fish and localized in the membrane of the tubular systems distributed extensively over the cytoplasm of chloride cells (McCormick, 1990, 1995, 2001; Kaneko et al., 1995, 2002). It is the major driving force for ion secretion and absorption and considered as a fundamental regulator of chloride cell proliferation and differentiation in teleost fish (Karnaky et al., 1976; Hootman and Philpott, 1979; Bindons et al., 1994; McCormick 1995, 2001). Na+,K+-ATPase activity can be controlled under aquaculture conditions to manipulate fish growth (Boeuf and Payan, 2001; Chang et al., 2001).

Types of gill chloride cells

One of the main characteristic of gill chloride cells is an acidic cytoplasm which is used for identification through histochemical techniques with dyes such as toluidine blue and hematoxylin and eosin. Several other alternative methods for staining have been demonstrated (Pereira and Caetano, 2009). Localization of the chrloride cells in the embryonic teleost fish differs from their localization in postembryonic stages (Jurss and Bastrop, 1995). During the early developmental stages, chloride cells have been found in the epithelia covering the body and yolk sac and are ion-secreting sites; however, in the juveniles and adults chloride cells are localized in the branchial and opercular epithelia of marine teleosts (Shelbourne, 1957; Shen and Leatherland, 1978; Ayson et al., 1994; Kaneko et al., 1995).

In freshwater teleosts, chloride cells have been suggested to play important roles in the uptake of ions and are the principal site of transepithelial Ca2+ and Cl- influxes (Foskett and Scheffey, 1982; Bindons et al., 1994; Lee et al., 1996a, 1996b). Studies indicate that the pavement cell is the site of Na+ uptake via channels linked electrically to an apical membrane vacuolar H+-ATPase (proton pump). During acidosis, the chloride cell surface area is diminished by an expansion of the adjacent pavement cells, resulting in decrease in the number of functional Cl-/HCO3-. During alkalosis, the chloride cell surface area is increased, which serves to enhance base equivalent excretion as the rate of Cl-/HCO3- exchange is increased (Perry and Laurent, 1989; Perry, 1997). The different models postulated for Na+ uptake in freshwater chloride cells are amiloride-sensitive electroneutral Na+/H+ exchanger with the driving force generated by Na+,K+-ATPase and carbonic anhydrase. Additionally, Na+ uptake occurs through an amiloride-sensitive epithelial sodium channel electrogenically coupled to proton pump (Hirose et al., 2003). In seawater teleosts, transcellular secretion of Cl- is achieved by different ion channels and transporters: Na+,K+-ATPase, Na+/K+/2Cl- cotransporter and a K+ channel (Hiroi et al., 1998; Hiroi et al., 2012).

On the basis of chloride cell location and response to seawater or freshwater transfer, two types of chloride cells have been identified in the gill filament and lamellar epithelia of several euryhaline species, such as the adult form of chum salmon (Uchida et al. 1996, 1997), eel (Sasai et al. 1998), and sea bass (Hirai et al. 1999). In euryhaline teleosts, filament and lamellar chloride cells

are thought to be important in seawater and freshwater adaptation, respectively (Kaneko et al., 1995, 2002). However, during early development differences in the distribution were demonstrated. In metamorphic larvae of Japanese flounder, although the gills are equipped with filaments and lamellae, chloride cells are distributed only in the filaments but not in the lamellae (Hiroi et al., 1998). Similarly, in the killifish a large number of chloride cells are detected in the gill filaments during early development with no chloride cells in the gill lamellae (Katoh et al., 2000; Katoh et al., 2001). Distinct seawater and freshwater types of chloride cells are demonstrated in killifish, localized mostly in a flat region of the afferent-vascular edge of the gill filaments. The apical membrane of chloride cells are invaginated to form a pit in seawater-adapted killifish, whereas it is flat or show projections with microvilli in freshwater-adapted fish (Katoh et al., 2001). In the air breathing fish, chloride cells are distributed in the gill lamella (Lin and Sung, 2003). Two different types of chloride cells, based on the size were revealed in the white fish with distribution mainly in the interlamellar region of the filament epithelium (Saadatfar et al., 2006). In addition to the gills, a large number of chloride cells are also reported in the opercular membrane. Interestingly, some chloride cells in the gills and opercular membrane of adult fish also form multicellular complexes (Katoh et al., 2000; Fiol and Kultz, 2007).

Hormonal regulation of gill chloride cells

Hormonal regulation of chloride cells and Na+,K+-ATPase are critical during migration of fish between fresh water and seawater and within estuaries, and is also important in stenohaline fish under variable environmental conditions. the hormonal control of chloride cells and Na+,K+-ATPase is critical to euryhalinity in fish. Chloride secretion appears to be under multiple hormonal control. Epinephrine, somatostatin, and the caudal neurosecretory peptide urotensin II, and prostaglandin inhibit chloride secretion while urotensin I, phosphodiesterase inhibitors, glucagon, and vasoactive intestinal peptide stimulate chloride secretion in chloride cell-containing tissues. Moreover, cortisol, growth hormone, insulin-like growth factor I, and thyroid hormones increase Na+,K+-ATPase and/or promote the differentiation of chloride cells (Degnan et al., 1977; Foskett and Hubbard, 1981; Foskett et al., 1982; Erikson et al., 1985; Van Praag et al., 1987; Uesaka et al., 1994; McCommick, 2001).

The growth hormone/insulin-like growth-factor axis promotes the development of branchial ionoregulatory functions that underlie ion secretion. Insulin-like growth-factors interact with insulin-like growth-factor binding proteins that modulate hormone activity (Breves et al., 2017a). Prolactin is the major regulator of ion and water transport in vertebrates, including fish. In teleosts, prolactin promotes phenotypes associated with freshwater acclimation; however, growth hormone promotes phenotypes associated with seawater acclimation (McCormick, 2001; Breves et al., 2016). Cortisol, under the control of ACTH support both freshwater and seawater acclimation (McCormick, 2001; Breves et al., 2016). Aquaporin proteins are important mediators of transepithelial fluid transport and cell volume regulation in vertebrate tissues and regulated in response to osmoregulatory demands. Branchial aquaporin levels in tilapia are modulated following changes in environmental salinity, with enhanced levels upon transfer from seawater to freshwater. Also, the study indicated that prolactin and cortisol act directly upon branchial epithelium to regulate aquaporin in tilapia (Breves et al., 2016). Euryhaline fish respond to variations in environmental salinity by modulating the levels of gene transcripts that encode effectors of ion transport (Fiol and Kultz, 2007; Breves et al., 2016). Recently, in tilapia, a regulatory link between prolactin and Clc Cl- channel was demonstrated (Breves et al., 2017b). Ion uptake mechanisms are diverse in fish species, linked to duplication events that have led to the presence of a multiple paralogous genes (Blondeau-Bidet et al., 2019).

Future perspectives

Salinity influences the amount of energy available for the growth by changing the energetic cost of ionic and osmotic regulation. The effects of salinity on fish growth vary greatly among teleosts, and Na+,K+-ATPase activity is generally lowest in fish living in a medium whose salinity is equivalent to that of the blood (Boeuf and Payan, 2001; Saoud et al., 2007; Blanco Garcia et al., 2015). A reduction in fish growth when reared in non-optimal salinity waters is due to an increase in Na+,K+-ATPase activity and concomitant energy expenditure, and vice-versa (Boeuf and Payan, 2001; Sampaio and Bianchini, 2002). As osmoregulation is an energy expensive process, understanding the mitochondrial rich chloride cell dynamics is one of the important aspects to control growth of the cultured fish. There has been an increasing demand for cost efficient rearing methods for cultured fish larvae and juveniles to accelerate growth. Several reports indicate that rearing of fish in optimum salinity result in improved growth performance by affecting NKA activity in chloride cells (Yoshikawa et al. 1993; Woo and Kelly, 1995; Sampaio aand Bianchini, 2002; Sangiao-Alvarellos et al., 2003; Laiz-Carrion et al., 2005; Blanco Garcia et al., 2015; Kitano et al., 2017). Our recent research with pearl spot maintained in recirculatory aquaculture system tanks indicated superior growth in brackishwater (15 ppt) when fed with 3% of the body weight, in comparison to other treatments. Previous studies in pearlspot indicated differential activation of ion transporters indicating its wide salinity tolerance and potential fish for aquaculture under different salinities (Chandrasekar et al., 2014). In Canara pearlspot, expression of osmoregulatory genes viz. sodium pump, Na+ K+ ATPase and prolactin receptor and osmotic stress transcription factor 1 revealed hyperosmotic stress induced nka and ostf1 gene upregulation and downregulation of prlr expression in the gills (CIBA, 2017). It is likely that changes in the activity of gill chloride cell modulates superior growth in pearlspot cultured in optimum salinity, as demonstrated in other euryhaline teleosts.

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