The role of aquaporins in the kidney of euryhaline teleosts

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Water balance in teleost fish is maintained with contributions from the major osmoregulatory organs: intestine, gills, and kidney. Overall water fluxes have been studied in all of these organs but not until recently has it become possible to approach the mechanisms of water transport at the molecular level. This mini-review addresses the role of the kidney in osmoregulation with special emphasis on euryhaline teleosts. After a short review of current knowledge of renal functional morphology and regulation, we turn the focus to recent molecular investigations of the role of aquaporins in water and solute transport in the teleost kidney. We conclude that there is much to be achieved in understanding water transport and its regulation in the teleost kidney and that effort should be put into systematic mapping of aquaporins to their tubular as well as cellular localization.

Keywords: kidney, aquaporin

INTRODUCTION

Multiple aquaporins have been functionally characterized and mapped along the nephron in the mammalian kidney, where they play a pivotal role in the maintenance of water homeostasis (Nielsen et al., 2002). Teleost kidneys are unable to produce hyperosmotic urine due to the lack of a loop of Henle, yet the role of aquaporins is suspected to be related to conservation of water in seawater (SW) and possibly excretion of water in freshwater (FW). In 2010 Cerdà and Finn summarized that 11 orthologs have been reported in whole kidney tissue (incl. vasculature and supporting tissues) of various teleosts: aqp-1aa, -1ab, -3a, -3b, -7, -8aa, -8ab, -9a, -10a, 10b, and -12. We have recently localized yet a paralog of aqp8 – termed aqp8b in the kidney of Atlantic salmon (Salmo salar) and rainbow trout (Oncorhynchus mykiss; Figures 1E,F). Only a few aquaporins have been localized in specific tubule cells, and their dynamics and functional role are far from known (Table 1).

FUNCTIONAL MORPHOLOGY OF THE KIDNEY IN EURYHALINE TELEOSTS

Freshwater-fish encounter osmotic load from the environment and the primary function of the filtering kidney is to produce large amounts of hypotonic urine. Salts are inevitably lost in this process as well as across gills and skin, which is compensated for by branchial and dietary NaCl uptake. SW fish are threatened to being predominantly secretory in FW to being predominantly secretory in SW. The function of the proximal segment(s) of the kidney tubule is somewhat controversial. There is, however, consensus that one primary function is secretion of Mg$^{2+}$ especially in marine and SW-acclimated species. Mg$^{2+}$ secretion involves apical exocytosis of vesicles enriched with Mg$^{2+}$ (Renfro, 1999). Accompanying fluid secretion may occur in both filtering and non-filtering nephrons but would be expected to occur particularly in SW fish.
in order to facilitate Mg$^{2+}$-secretion in tubules with low GFR. In FW-kidneys it could play an additional role in excretion of excess water (Beyenbach, 2004). With regard to NaCl and water transport, available data are more diverging. In some species, there is evidence that the proximal segments of both FW and SW fish are responsible for absorption of Na$^+$ and Cl$^-$ as well as glucose and other important osmoles (Nishimura and Imai, 1982; Dantzler, 2010). The apical Na$^+$-entry pathway into proximal cells is yet unclear but may involve Na$^+$/H$^+$-exchange (Braun and Dantzler, 1997; Ivanis et al., 2008) and Na$^+$-glucose cotransporters (SGLT1). The role of SGLT1 has generally not been investigated much in teleost kidneys but its mRNA expression is indeed very high in some species, including S. salar, where it may contribute to absorption of Na$^+$ and Cl$^-$. Additionally, SGLT1 may play a role in NaCl absorption in the proximal segments of both FW and SW fish. This is supported by the expression of SGLT1 in proximal tubules, which is more abundant in FW-kidneys than in SW-kidneys.

Distal tubules and collecting ducts together make up a variable percentage of whole nephrons in different fish (Katoh et al., 2008) and the primary activity here is reabsorption of NaCl in both FW and SW. This is favored by extensive expression of basolateral Na$^+$, K$^+$-ATPase (Katoh et al., 2008) and NaCl cotransporter (NCC; Kato et al., 2011), and basolateral kidney-specific Cl-channels (Miyazaki et al., 2002). Accordingly the distal segment is absent in the majority of truly marine species (Hickman and Trump, 1969). In FW fish the distal segments are proposed to have low water permeability in order to minimize water reabsorption and promote the formation of hypotonic urine (McDonald, 2007). Upon acclimation to SW, the fractional reabsorption of water increases along the nephron by increasing tubular water permeability as seen in mammalian collecting tubules. Reabsorption of NaCl may promote the osmotic removal of water – thereby creating isotonic urine primarily consisting of MgSO$_4$ and other unwanted osmoles (Beyenbach, 2004).

Surprisingly little information is available about the molecular mechanisms of tubular water movement and how it is controlled in fish. Among the most obvious candidates for renal control are arginine vasotocin and angiotensin which have vasoreactive effects that...
Table 1 | Overview of aquaporin expression and localization in fish kidneys.

| D. rerio* | S. salar | O. mykiss | O. mossambicus | A. anguilla | A. japonica | D. labrax | S. aurata | S. sarba | A. schlegeli | P. annectens* |
|-----------|---------|-----------|----------------|-------------|-------------|-----------|-----------|---------|--------------|--------------|
| aqp1aa    | m       | m/p, SW (↑) | p              | m/p, SW (↑) | –           | m/p       | –         | m/p     | m/p          | m, SW (↑)     |
| TS        |         | PT        |                | Unknown     | A           | Known     | Known     |         |              |              |
| SL        |         | A + BL    |                | A           | A           |           |           |         |              |              |
| aqp1ab    | –       | m/p, SW (↑) | p              | m, SW (↑)   | m           |           |           |         |              |              |
| TS        |         | PT (PW)   |                | PT + DT (SW)|           | SA + A    |           |         |              |              |
| SL        |         | m/p       |                | m/p         | m/p         |           |           |         |              |              |
| aqp2      |         | m/p(activation) LDT | A   |
| TS        |         |           |                |             |             |           |           |         |              |              |
| SL        |         |           |                |             |             |           |           |         |              |              |
| aqp3a     | m       | m, SW (↑) | m, SW (↑)      | m, SW (↑)   | m/p         |           |           |         |              |              |
| aqp3b     | –       | –         | m/p, SW (↑)    | –           |             |           |           |         |              |              |
| TS        |         |           |                |             |             |           |           |         |              |              |
| SL        |         |           |                |             |             |           |           |         |              |              |
| aqp7      | m       |           |                |             |             |           |           |         |              |              |
| aqp8aa    | m       | –         | –              |             |             |           |           |         |              |              |
| aqp8ab    | m       | –         | –              |             |             |           |           |         |              |              |
| aqp8b     | –       | m/p       | p              |             |             |           |           |         |              |              |
| TS        |         | PT (PW + SW) |                |           |           |           |           |         |              |              |
| SL        |         | BL        |                |             |             |           |           |         |              |              |
| aqp9a     | m       |           |                |             |             |           |           |         |              |              |
| aqp10a    | m       |           |                |             |             |           |           |         |              |              |
| aqp10b    | m       | m, SW (↑) | m, SW (↑)      | m           | –           |           |           |         |              |              |
| aqp12     | m       |           |                |             |             |           |           |         |              |              |

Reference

*All species listed in the table are euryhaline with the exception of D. rerio and P. annectens which are freshwater fishes. TS, tubule segment; SL, subcellular localization; m, mRNA expression; p, protein expression by immunocytochemistry or immunoblotting; –: not detected; blank: not investigated; ↑ or ↓: up- or down-regulation of mRNA upon seawater exposure; A, apical membrane; SA, subapical membrane; BL, basolateral membrane; PT, proximal tubules; DT, distal tubules; LD'T, late distal tubules; FW, freshwater acclimated fish; SW, seawater acclimated fish.
Aquaporins in teleost kidney

**AQUAPORIN 1**

Aquaporin 1 exists as two paralogs in teleosts: aqp1aa and aqp1ab (Cerdà and Finn, 2010). The first report of kidney aquaporins was made by Martinez et al. (2005), who found two classic aquaporins (aqp1 and aqp1dup – now aqp1ab) and one aquaglyceroporin (aqp3 – now aqp1b, Tingaud-Sequeira et al., 2010) in FW- and SW-acclimated European eels (Anguilla anguilla). The mRNA expression of these declined during SW-acclimation – and also partly during the pre-migratory metamorphosis from the yellow to silver form. A somewhat similar expression pattern was reported in black porgy (Acanthopagrus schlegeli; An et al., 2008), where aqp1 expression varied according to salinity in the order: 10% SW > FW > SW. This response is opposite of what would be expected, if these aquaporins are involved in tubular water absorption, and accordingly the authors concluded that aqp1 may be involved in water secretion. In contrast, the expression of aqp1 mRNA in the kidney of sea bass (Dicentrarchus labrax) was four to five times higher in SW- than in FW-acclimated fish (Giffard-Mena et al., 2007). In Atlantic salmon, Tipmark et al. (2010) reported increasing mRNA levels of aqp1aa during SW-acclimation (and smoltification), but this was accompanied by a concomitant decrease in the mRNA of aqp1ab, suggesting that these paralogs play differential roles in water homeostasis in the Atlantic salmon kidney. The bass and salmon studies agree well, since the sea-bass aqp1 ortholog is more similar to the aa- than the ab-ortholog of Atlantic salmon aqp1. In stenohaline zebrafish kidney only one aqp1 paralog is found (aqp1aa), which adds further complexity to the physiological roles of aqp1 (Tingaud-Sequeira et al., 2010). At the moment it is unclear to what degree the diverging results obtained for aqp1ab can be explained by species differences or the varying experimental designs.

There is very little knowledge of the localization of Aqp1 protein isoforms along the teleost nephron. Martinez et al. (2005) found positive immunoreaction in the eel kidney using a homologous antibody. Staining was generally present in the endothelium in yellow eels; but in both FW and SW silver eels a “subset” of renal tubules (presumably proximal) exhibited strong staining in the brush border zone of epithelial cells. No attempts were made to further determine the segmental origin of these tubules. Aqp1La also appeared in apical localization of renal tubules of SW-acclimated gilthead sea bream (Sparus aurata, Cerdà and Finn, 2010). Initial studies of rainbow trout show a clear segmentation of Aqp1 protein isoforms in renal tubules. Irrespective of salinity, Aqp1La is present in the apical and basolateral membrane of proximal tubules, judged from the intensity and pattern of Na+, K+-ATPase localization (Figures 1A,B). The Na+, K+-ATPase is present basolaterally in all tubule segments but is more abundant in the highly folded membranes of distal and collecting tubules than in proximal segments of the nephron (Katoh et al., 2008) allowing differentiation between tubule segments. Aqp1ab is found in the apical brush border of proximal and distal tubules in SW-acclimated rainbow trout (not shown), while being predominantly withdrawn to a subapical position in proximal tubules in FW-acclimated rainbow trout (Figures 1C,D). This suggests that trafficking may contribute to the regulation of this isoform as has been reported for fish oocytes (Fabra et al., 2005, 2006; Chabé et al., 2011) and also discussed for intestinal Aqp1ab elsewhere in this Special Topic (Madsen et al., in review).

Only one study has reported hormonal effects on kidney aqp1 mRNA. Martinez et al. (2005) found that expression of aqp1aa and aqp1ab in yellow eels was suppressed by cortisol, whereas the hormone had no effect in silver eels, where the mRNAs were already at lower levels. This confirms the conception of cortisol being a SW-adapting hormone in eel.

**AQUAPORIN 2**

In strong contrast to mammals, this isoform has not been detected in teleosts (Cerdà and Finn, 2010). However, one study has documented aquaporin 2 in the kidney of African lungfish (Protopterus annectens; Konno et al., 2010), where mRNA and protein levels increased during aestivation. Moreover, Aqp2 was localized to the apical membrane of late distal tubule cells, where the vasopressin/vasotocin-V2 type receptor was present basolaterally. This suggests that water deficiency in the fish world may have promoted convergent evolution of a mechanism for renal water conservation similar to that responsible for urine concentration in mammals (Nielsen et al., 2002).

**AQUAPORIN 3**

The aquaglyceroporin aqp3 exists as duplicate paralogs in zebrafish: aqp3a and aqp3b (Cerdà and Finn, 2010) but only aqp3a mRNA is present in the kidney of zebrafish. Aqp3b mRNA was first reported absent from kidneys of SW-acclimated eel using Northern blotting (Cutler and Cramb, 2002). Later, the same group used RT-PCR to detect low levels of aqp3b mRNA in renal tissues which increased upon SW-acclimation (Cutler et al., 2007). This agrees with tilapia (Oreochromis mossambicus), where aqp3a mRNA is present in higher levels in SW- than FW-kidney (n = 1; Watanabe et al., 2005), and with Atlantic salmon where renal aqp3a mRNA increased >10-fold within 24 h after FW- to SW-transfer and stayed elevated for 2 weeks (Tipmark et al., 2010). The same trend was seen in sea bass (Giffard-Mena et al., 2007), though not confirmed in a subsequent study (Giffard-Mena et al., 2008). In silver sea bream (Sparus sarba) the Aqp3a protein was detected by immunoblotting using homologous antibodies but no change was seen upon acclimation to a range of salinities (Deane and Woo, 2006). Finally, Kim et al. (2010) found no expression of aqp3b in kidney of Japanese eel (A. japonica). From this comparison, it seems that the aqp3b isoform is either absent or present in rather low levels in fish kidneys. In those species where aqp3a is expressed, the abundance is higher and mostly increases in response to hyperosmotic conditions. Thus Aqp3a may have a role in water conservation. A supplemental role in glycerol and urea transport is another putative function of Aqp3 (Maclver et al., 2009).

There is only one preliminary report of renal Aqp3 localization. Using a homologous antibody Cutler et al. (2007) detected Aqp3b protein in the apical domain of eel renal tubule cells (Cutler et al., 2007). This contrasts the basolateral location in distal segments of
the mammalian kidney, where it serves a role in cellular water exit (Nielsen et al., 2002).

**AQUAPORIN 8**

In mammals, the role of renal AQP8 is unclear, since it is predominantly located in intracellular vesicles in proximal tubule and collecting duct cells (Elkjer et al., 2001). In addition to water, this isoform may also transport ammonium and thus be involved in acid–base control (Liu et al., 2006). In fish, there is very little information regarding the expression and function of this isoform – mostly related to intestinal function (Cutler et al., 2009; Kim et al., 2010; Madsen et al., in review). In zebrafish kidney, two paralogs of aqp8 are expressed: aqp8aa and aqp8ab (Tingaud-Sequeira et al., 2010), whereas no expression of these paralogs was detected in Atlantic salmon (aqp-8aa and -8ab: Tipsmark et al., 2010) or Japanese eel (aqp8aa: Kim et al., 2010). However, we have recently discovered a third paralog of aqp8 (aqp8b) in salmon, which is abundantly expressed in both intestinal and renal tissue. This paralog is also found in other teleost species but surprisingly not in the intestine or kidney of zebrafish (Cerdà and Finn, 2010; Tingaud-Sequeira et al., 2010). Preliminary results using homologous antibodies show a predominant staining of the basolateral membrane of some renal tubule cells in FW-acclimated rainbow trout (Figures 1E,F). We suspect that these tubules are proximal based on the moderate basolateral staining for Na+, K+-ATPase. This is the first demonstration of a basolateral AQP8 in fish kidney tubules, which may serve together with the Aqp1aa isoform as important exit pathways for reabsorbed water.

**AQUAPORIN 10**

Aqp10, another aquaglyceroporin, is not expressed in the kidneys of mammals but is located in the apical membrane of the small intestine, where it is suspected to participate in transport of water and small solutes (Hatakeyama et al., 2001; Mobasheri et al., 2004). In zebrafish kidney, aqp10 is expressed as two paralogs: aqp10aa and aqp10ab (Cerdà and Finn, 2010). Orthologs of aqp10bb were also identified in kidneys of SW-acclimated gillhead sea bream (sbaap: Santos et al., 2004), European eel (apec: Martínez et al., 2005), and Atlantic salmon (Tipsmark et al., 2010). In sea bream, aqp10bb mRNA was demonstrated by in situ hybridization in tubule cells of undefined origin. Functional assays using Xenopus oocytes have further shown that this aquaglyceroporin is capable of water, glycerol and urea uptake (Santos et al., 2004; Maclver et al., 2009). In the eel study, SW-acclimation was associated with lower levels of aqp10b mRNA in yellow eels, whereas silver eels showed no response. In salmon, the effect of salinity was opposite; aqp10b expression was increased fivefold at 8 days after transfer to SW. Even though species differences seem to exist, all available evidence points to a salinity dependent expression and thus a role of Aqp10b in fluid handling in the teleost kidney. The endocrine regulation of this isoform remains unknown.

**ADDITIONAL AQUAPORINS**

Aquaglyceroporins 7 and 9 and one unorthodox aquaporin 12 have been reported in the zebrafish kidney (Tingaud-Sequeira et al., 2010) but no information is available on their functional characteristics, tubular localization, nor their expression dynamics. In mammals, AQP7 is present in brush border membranes of proximal tubules, where it is suspected a role in glycerol metabolism (Noda et al., 2010). AQP9 and -12 have not been located in the kidney of mammals (Nielsen et al., 2002).

**CONCLUSION AND PERSPECTIVES FOR FUTURE RESEARCH**

Euryhaline teleosts have a capacity to acclimate to salinities ranging from strongly hypotonic to strongly hypertonic. In doing so their kidney function is dramatically altered. Despite this fact, surprisingly few studies have addressed the role and dynamics of aquaporins in fish kidneys. These have so far only probed for transcriptional regulation of few aquaporins and found interesting though conflicting results. Most data have demonstrated apical aquaporin expression in renal tubules, and future studies are encouraged to systematically investigate the specific protein isoforms, their dynamics and cellular expression as well as their hormonal and environmental regulation. This review has tried to show that there is still much to learn about water homeostasis in fish.

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